



सत्यमेव जयते

INDIAN AGRICULTURAL  
RESEARCH INSTITUTE, NEW DELHI.

I. A. R. I. 6.

MGIPC—SI—6 AR/54—7-7-54—10,000.







THE QUARTERLY REVIEW  
*of* BIOLOGY

VOLUME II  
1936

**319128**  
**[AR]**

*Published by*  
**THE WILLIAMS & WILKINS COMPANY**  
**BALTIMORE**  
**U. S. A.**

# THE QUARTERLY REVIEW OF BIOLOGY

~

RAYMOND PEARL, *Editor*  
*The Johns Hopkins University*

ASSISTED BY

R. W. HEGNER  
*Contributing Editor*  
*The Johns Hopkins University*

MAUD DEWITT PEARL  
*Assistant Editor*

## ADVISORY BOARD

ANATOMY.....	LEWIS H. WEED.....	<i>The Johns Hopkins University</i>
ANTHROPOLOGY.....	A. L. KRONER.....	<i>University of California</i>
BEHAVIOR AND COMPAR-		
ACTIVE PSYCHOLOGY....	K. S. LASHLEY.....	<i>University of Chicago</i>
BOTANY.....	IRVING W. BAILEY....	<i>Harvard University</i>
CYTOLOGY.....	CHARLES W. METZ.....	<i>Carnegie Institution</i>
ECOLOGY.....	WILLIAM MORTON WHEELER.....	<i>Harvard University</i>
EMBRYOLOGY.....	E. G. CONKLIN.....	<i>Princeton University</i>
EXPERIMENTAL		
MORPHOLOGY.....	ROSS G. HARRISON.....	<i>Yale University</i>
GENERAL PHYSIOLOGY	{ LAWRENCE J. HENDERSON.....	<i>Harvard University</i>
	{ G. H. PARKER.....	<i>Harvard University</i>
GENETICS.....	{ R. A. EMERSON.....	<i>Cornell University</i>
	{ T. H. MORGAN.....	<i>California Institute of Technology</i>
GEOGRAPHICAL DISTRI-		
BUTION AND TAXON-		
OMY.....	ALEXANDER G. RUTHEVEN.....	<i>University of Michigan</i>
PALEONTOLOGY.....	JOHN C. MERRIAM.....	<i>Carnegie Institution</i>
RUSSIAN BIOLOGICAL		
LITERATURE.....	W. W. ALPATOV.....	<i>University of Moscow</i>
ZOOLOGY.....	FRANK R. LILLIE.....	<i>University of Chicago</i>

# CONTENTS

No. 1, MARCH, 1936

	PAGE
Playing With a Dog.....	<i>E. S. Russell</i> 1
Whitehead's Philosophy of Organism. An Introduction for Biologists..	<i>W. E. Agar</i> 16
The Functions of the Pyramidal Tracts.....	<i>Clyde Marshall</i> 35
The Gene, Its Function and Its Meaning in Genetics.....	<i>W. F. H. Ströer</i> 57
Problems in the Classification of Neonate Activities.....	<i>Karl C. Pratt</i> 70
New Biological Books:	
Brief Notices.....	81

No. 2, JUNE, 1936

The Black Widow Spider... ..	<i>Fred E. D'Amour, Frances E. Becker and Walker Van Riper</i> 123
The Problem of Cyclopia. Part I.....	<i>Howard B. Adelman</i> 161
Morphogenesis of the Shoulder Architecture. Part IV. Reptilia..	<i>A. Brazier Howell</i> 183
The Halophyte Problem in the Light of Recent Investigations.....	<i>V. J. Chapman</i> 209
New Biological Books:	
Brief Notices.....	221

No. 3, SEPTEMBER, 1936

Characters Common to Higher Primates and Characters Specific for Man. First Part.....	<i>Adolph H. Schultz</i> 259
The Problem of Cyclopia. Part II.....	<i>Howard B. Adelman</i> 284
Aberrant Feeding Behavior Among Insects and Its Bearing on the Development of Specialized Food Habits.....	<i>Charles T. Brues</i> 305
The Principles of Biocoenology.....	<i>G. F. Gause</i> 320
New Biological Books:	
A Notable Contribution to Entomology.....	<i>William Morton Wheeler</i> 337
Brief Notices.....	341

No. 4, DECEMBER, 1936

Sexual Photoperiodicity.....	<i>Thomas Hume Bissonnette</i> 371
The Spinal Accessory Nerve and Its Musculature	
.....	<i>William L. Straus, Jr. and A. Brazier Howell</i> 387
The Nutritional Requirements of Bacteria.....	<i>William Burrows</i> 406
Characters Common to Higher Primates and Characters Specific for Man. (Continued)	
.....	<i>Adolph H. Schultz</i> 425
New Biological Books:	
Brief Notices.....	456
The Prices of Biological Books in 1936. ....	<i>Raymond Pearl and Maud DeWitt Pearl</i> 492
Index to Volume 11.....	495



# THE QUARTERLY REVIEW *of* BIOLOGY



## PLAYING WITH A DOG

By E. S. RUSSELL

*Berkhamsted, England*

THE title of this paper may appear frivolous. It has been chosen deliberately, with a serious purpose. I propose to show how an attentive study of the behavior of a dog, as it plays and as it goes about the ordinary business of its life, may bring to light some general principles of animal behavior which are of the profoundest importance.

In a dog's world its master is the dominant figure, and its relations with its master, as for example in play, make up a big slice of its life. It is not quite true to say that a dog never plays alone, but play is predominantly a social affair; a dog plays with other dogs, other familiar animals and with human beings. I have known dogs, both of them as it happens Toy Yorkshire Terriers (females), which played when alone. Both these bitches would pick up a small object and throw it a little distance with a sideways jerk of the head, running after it to pick it up and throw it again. (Their pedigrees show that they had no common ancestors in four generations.) The "killing" game referred to below might also be regarded as solitary play. As a rule, however, a

dog must have a partner in its play, and it is with the games my dog Gina plays with me that I shall begin. Gina is a smooth haired Fox Terrier bitch, with an admixture of rough haired ancestry, and at the time of writing (August, 1935) nearly four years old. She has been under general observation by my wife and myself since she was six weeks old. No attempt was made to train Gina in any elaborate way; she was not subjected to experiment in the laboratory; she was in fact allowed and encouraged to be the experimenter as well as the experimentee. The observations here recorded are for the most part transcribed from notes jotted down from day to day.

### THE BALL GAME

When about a year old, Gina was taught to retrieve a ball. It is natural for a terrier to chase and pick up a ball that is thrown, but some slight training is required to ensure that the ball is brought back. This was quickly achieved by ignoring the ball if dropped at some distance, but picking it up and throwing it again if it was dropped within reach. The command "Fetch" was also asso-

ciated with finding and bringing back the ball. This retrieving behavior was very rapidly established, and soon underwent a significant extension, for Gina would spontaneously seek out her ball and bring it to us to throw. If we paid no attention she would drop the ball near us, sometimes on our foot, and bark vigorously. The game in fact soon became an obsession with her, and if permitted she would play it in and out of season.

Now in this simple everyday behavior there are many things that deserve close attention. The whole action of chasing and retrieving the ball is a typical example of directive or "goal-seeking" behavior, and as such shows certain characteristics which are found in all behavior. First, it has all the objective marks of attentive behavior. If I pick up the ball, Gina approaches in a state of tension and alertness, ears pricked up, and her eyes fixed upon the ball. She is irresponsive to other stimuli, ignores another dog yapping at her side, or the call of her mistress. She follows with the closest attention the slightest movements of the hand holding the ball. This concentrated attention on the ball is particularly noticeable if it is lying on the ground near my foot and I am about to kick it; the slightest preparatory movement of the foot is closely observed by the dog and followed by a slight movement of its head in the same direction. (That a dog responds to very slight, even involuntary, cues given by the experimenter is of course now well known, but failure to recognize this fact caused some confusion in the early days of laboratory experiment.) When I throw or kick the ball, the dog sets off in the direction indicated by the movement of my hand or foot, and when she comes within reach she snaps it up. Through long practice she has become expert at catching it on the bounce. If the ball goes out of

sight in the long grass Gina searches for it, hastily quartering the area with her stern in the air, her tail moving rapidly with full steady strokes, her nose to the ground. This particular tail action is so regular and typical that one can always tell from it that she is seeking or hunting. She may find the ball, if she passes close to it, probably by smell, and then she brings it back to me; or the search may last for some minutes and yield no result, when she returns to me and barks, just as she does when she wants me to play ball with her.

We may single out the following characteristics of this train of action as typical of behavior in general—(1) it is an activity of the animal as a whole in relation to something outside it; (2) the activity of the animal is concentrated on the course of action which is being pursued; (3) the activity is directed towards a particular end-state or completion, the retrieving of the ball; (4) it shows persistence, for if the ball is not found at once the search is pursued till the likely ground has been covered, perhaps more than once; (5) cessation or continuance of the action is governed by result; if the ball is found, searching stops; until it is found, searching goes on, at least for a time; (6) it shows variety of effort, not only in the actual searching, but more conspicuously in the shift over to a new type of action if the search has proved unavailing, for the return to me is undoubtedly to be regarded as an indirect method of obtaining possession of the ball.

Although this description is couched in objective terms, referring only to observable characteristics of the action, it bears a close resemblance to the well known definitions of attentive and conative behavior given by such psychologists as Hobhouse (1926), Stout (1913), and McDougall (1913). It seems to me quite impos-

sible to give an adequate description of behavior without reference to its directiveness, its aiming at a specific and definite end-state or completion. I say "end-state" deliberately and not "end," because of the ambiguity inherent in the latter word. The distinction between end-state and end has been so clearly brought out by Stout that I cannot do better than quote him. The word *end*

may mean either (1) actual satisfaction of conation, or (2) the conditions of satisfaction as they appear to conative consciousness before the satisfaction is actually and completely attained. In sense (1) the term *end*, whatever else it may imply, implies also its ordinary literal meaning of termination or cessation. . . . The end, in this sense, implying actual satisfaction, and with satisfaction the cessation of the conative process, may be called by way of distinction the *end-state* or *terminus*. We may then confine the word end to its second meaning as *object* of conative consciousness—the conditions of satisfaction as apprehended by the subject before actual attainment (1913, pp. 123, 124).

While there is more in Gina's behavior than the "closure" of an unstable dynamic system, as Gestalt psychology would have us believe, it is not necessary to assume that she clearly conceives the end or goal of her behavior and acts with deliberation and forethought. Psychologically, her activity appears to lie at a lower level altogether; the connection between perception, impulse and action is more direct; her "mental" activity is, as the classical psychologist would say, perceptual rather than conceptual, just as our own is when we are actively engaged in playing tennis. A teleological explanation of her behavior, that is to say an explanation in terms of ends, is in fact unnecessary and, probably, psychologically unsound. We should therefore in describing her behavior use the word *end-state* rather than *end*, in accordance with the important distinction drawn by Stout.

By using the neutral word end-state we

avoid the teleological implications of the word end. What we cannot leave out of a characterization or definition of behavior, without emasculating it, is the objective phenomenon of directive, persistent activity which tends actively towards the attainment of a specific and definite end-state or completion.

It would be out of place here to attempt the demonstration that behavior in general shows the same objective characteristics which we have noted in Gina's retrieving game, namely whole-action with reference to a specific end-state, persistency with varied effort, action governed by result. It is sufficient to point out that these objective marks of behavior stand out clearly in Jennings' classical account of the pursuit of one *Amoeba* by another (1915).

So far we have considered mainly the executive or motor aspect of Gina's behavior in retrieving a ball; let us now turn to its perceptual aspect.

Before Gina was trained to play with a ball, it was to her an indifferent or neutral object—it elicited no attention, no behavior. In the course of training it became a significant object, or, to introduce here a convenient technical term, it acquired *valence*, became a *valent* object. (On the previous use of this term see below.) By this I mean simply that Gina manifested attention and behavior in relation to it. Now soon after a ball—any ball—acquired valence, other objects, *which could be used in the same way*, also acquired the same or similar valence. On a country walk she would pick up and deposit at my feet stones, pine-cones, sticks and broken boughs. I have known her dig out a half-buried stone and bring it, or pull at a root to break it loose. The picking up of sticks and stones is no doubt due to the fact that in the absence of a ball I may throw these for her. Other objects which have been noted as having



ball-valence are an orange, a gooseberry, a bottle cork, a raw potato, a box of safety matches, a child's wooden cube, a clean dry bone, and what is really rather extraordinary, a rubber boot-sole and a long-handled hearth brush. All these objects she has on occasion brought to me and dumped at my feet, with the obvious expectation (clearly deducible from her attitude and behavior) that I should throw them for her to retrieve.

Now these objects have nothing in common, except that they are "pick-up-able" and potentially retrievable, yet they have the same or similar valence. We may say then that they are *equi-valent*, for they elicit the same kind of behavior.

What can we deduce from these facts? Not, certainly, that these objects look alike to the dog—definite evidence will be given below that the dog can distinguish clearly between different forms and appearances. Nor does there appear to be any common sensory quality among them—they are diverse in form, color and smell; they have in common only a certain restriction in size, and the quality of moveableness so that the dog can easily pick them up and carry them. It is then their *functional* value, functional valence, which makes them stand out in the dog's perceptual world, causes the dog to notice them and make use of them.

That the dog does not confuse these objects with one another is demonstrated by two simple observations. First, there is for Gina a definite order of preference among her balls proper; one type in particular, a hard black rubber ball, is so obviously preferred before all others that it is always known to us as "Gina's best ball." Some other balls, especially soft ones, possess so little valence that she is apt to drop and lose them after a little while. The second observation is the following:

Playing with a square piece of wood which I throw to her, G. loses it. Hunts for it, comes across and looks at a piece of firewood (a thin piece of wood some five inches long) with which she has played earlier in the day, but does not pick it up. A minute or two later finds a second square piece similar to the first, which she picks up and brings to me. 10.6.35.

Before passing on to describe another kind of play, I wish to refer in a preliminary way to the most important fact about valence, namely that it is relative to the attention or "interest" of the animal at the moment. This is rather prettily shown by a very simple observation which I transcribe with some expansions from a note made on 18.7.35.

I take Gina up the garden, playing ball with her. When she nears the collection of stakes and odd wood lying on the grass which previous experience has shown her to harbor voles, she runs there, still holding ball; in a few seconds she drops ball and goes nosing for voles, wagging her tail in the typical hunting or seeking manner. Pays no attention to the ball, even when I pick it up and throw it for her.

The valence of the ball is therefore dependent upon momentary attention or "interest"; when this is diverted to another object, eliciting a new course of action, the valence of the ball drops to zero. Thus it is attention or interest that essentially determines response to particular objects, rather than the objects *per se*. It is not of course denied that the mere sight of an object may directly arouse interest and attention, as when Gina, walking quietly along, suddenly lights on her ball and immediately seizes it. But in one way or another valence and attention are intimately bound together.

#### THE PENNY TRICK

I have described in another place (1934) how a penny became a valent object in Gina's perceptual world, acquiring the value of a means towards acquiring cheese, of which she is inordinately fond. She was taught in October or November

1932 to retrieve pennies, receiving as a reward a little piece of cheese, and shortly afterward she developed the habit of looking for pennies and bringing them in the expectation of reward. She would retrieve any coin, from a sixpence to a half-crown, thrown to her. Not only so, but other small objects acquired valence as means towards cheese. Here are some notes, made at the time.

19.1.33. I place penny in crevice of chair; Gina goes and digs it out. Afterwards she goes twice to chair to look for penny. Later, no penny being available, she brings me a bottle cork and drops it at me. I give her cheese; she brings cork again. Five minutes later, I throw her the cork; she brings it back as she would a penny and is given cheese. Goes and looks for cork or penny; again looks in chair.

20.1.33. Cork again brought at dinner time. Did not bring a large spoon which fell off table, nor when it was thrown.

22.1.33. Small brass hook brought for cheese—spontaneously.

11.9.33. At dinner, during meat course, Gina found box of book-matches on floor and brought it for reward; she was given a small piece of meat. She did this several times. Later I fetched a piece of cheese rind. Gina obviously expected me to throw a penny—her usual response to the presence of cheese—but when I pointed out the book-matches she brought them as she would a penny, retrieving them when thrown, dropping them as she does a penny, to attract attention.

It appears from these incidental observations that the response is not specifically to a penny, but extends to other coins and to other small objects, which are used as functionally equivalent to a penny, are therefore, in our nomenclature, *equivalent* with it. The basis of *equivalence* in this case appears to be the small size of the objects used.

Equivalence is shown also in another kind of play, which consists in vigorously shaking and "killing" a glove, a rubber mat, a velvet polishing pad, a sock or a rolled-up stocking, and other similar things. The action is similar to that

employed by Gina in killing a vole, and this play is probably to be interpreted as the killing of a substitute rat or vole or other small prey. A favorite article employed in this "killing" game is the long-handled hearth-brush mentioned above as being used as a "retrievable." It is more usually employed in the killing game. It has had for Gina a peculiarly strong attraction from her earliest youth.

It appears from this that one and the same object may, at different times, have a different valence, being employed in different games. Another case of change of valence is the use of a bottle cork either as a retrievable, with ball-valence, or as a means towards cheese, with penny-valence. The two actions, retrieving pure and simple, and bringing an object for reward, are of course very similar, but differ in certain details related to their "intention." Thus one is never allowed to pick up an object having penny-valence, if Gina can help it, while a ball-object is meant to be picked up.

I mentioned above that a clean dry bone may have ball-valence. I have recorded a case (1934) where a dry bone had, to all appearance, a pup-valence, and I may briefly recapitulate the facts here. Gina when exhibiting definite signs of pseudo-pregnancy dug up a buried bone and lay beside it for three hours, growling if approached, but not grabbing it as she would had she been treating it as food. She brought it into the house and curled herself round it. In the evening she dug a hole and buried it. Clearly the bone was treated during the day as functionally equivalent to a pup.

#### BURYING FOOD

A bone, if not completely bare and dry, has of course normally a high food valence. As such it figures in the habit shown by dogs (and some other car-

nivores) of burying food. This form of behavior is in all probability "instinctive" or independent of experience (Pitt, 1927), and as such it is curiously stereotyped or rigid in the details of its carrying out. Normally a dog buries its bone in soft earth, scraping a hole with its fore-feet. The food is placed in the hole with its mouth, and earth pushed over it with its nose. I have never seen a dog cover over the food by scratching—invariably the nose is used, in typical sweeping motions towards the food. The end-state aimed at, though not always achieved, is the covering of the food from sight. The action may be carried out in typical form in unusual environments and with unusual material. Thus I have noted Gina "burying" a piece of food by pushing over it with her nose some withered grass which was still attached by the root. On another occasion she buried food up against a boor-scraper, covering it neatly with straw and grass-stems pushed over it with the nose. The action may be carried out even indoors; thus on 14.8.32 Gina tried to bury a piece of biscuit on the dining room hearth, which is tiled, by pushing over it with her nose the plug and lead of the electric fire. The biscuit was, however, quite incompletely covered. A male Toy Yorkshire which we had used to bury sweets, biscuits and other tit-bits under cushions and in chairs, moving them to another spot if we threatened to take them.

Here is another case, noted on 12.9.32. "Gina takes piece of dog biscuit, leaps on bed, lays it on top blanket, sweeps blanket with her nose radially towards biscuit, exactly as if pushing earth over it. Instinct satisfied if biscuit by chance is pushed under pillow or down crevice between bed and wall, i.e., out of sight, more or less." In this and some other "abnormal" cases there was no pre-

liminary digging or scratching with the feet.

I have dwelt on these details because, though not strictly relevant to our main theme, they illustrate an interesting feature of instinctive behavior, its tendency to become independent of the normal perceptual situation and to be carried out in more or less routine form almost as a symbolic or ritual action.

According to Miss Pitt (1927) dogs do not usually dig up and eat buried food; this is not my experience with the three dogs (Gina and two Toy Yorkshires) I have observed in this connection. Not only did they usually select with care a "suitable" spot in the garden for their burying operations, but they very often sought out the spot afterwards and dug up the food. For a rather remarkable case of topographical memory for buried food exhibited by Gina after a lapse of 24 hours I may be permitted to refer to my book (1934, p. 6). However, the main fact about burying to which I wish to draw attention is that it has reference to a class of objects, namely surplus food, for all sorts of food may be buried as well as bones, and, so far as some dogs are concerned, nothing but food objects. Functional value, functional valence, is again decisive.

#### PERCEPTUAL WORLDS

In all the cases we have described, the ball game, the penny game, the "killing" game, and the burying behavior, it is important to note that valence is not a quality of objects *per se*, independent of the dog; it is the dog's "interest" or need or "intention" that essentially determines what objects (or what characteristics of objects) shall possess valence. To Gina attracted by an area signifying volcs a ball loses all its valence; to a dog satiated with food even meat has no positive valence and may even acquire

negative valence, causing aversion. It is the fact of the relative nature of valence that renders intelligible the circumstance that the same object may have different valence at different times.

A second point to note is that, in many cases at least, the initiative, so to speak, rests with the dog, who actively singles out, pays attention to, such objects as for the moment are significant in relation to its needs or interest. The valent objects need not be actually present; the dog then goes and looks for them.

The general picture of the relation between the dog and its perceptual or behavioral environment which these observations give us is very different from that which would be furnished by a physiological approach. The facts do not seem to fit in with the theory that behavior is reducible to simple stimulus-response relations, considered as physico-chemical events. It would appear that neither stimuli taken separately, nor patterns of stimuli (wholes) are the real determiners of behavior, but only such perceived objects or events as possess valence in relation to the dog's psychobiological state at the moment.

It is a significant fact, to which sufficient attention is rarely given, that the number and kind of valent objects or events in an animal's environment are distinctly limited—to many physical and chemical stimuli impinging on its sense-organs it makes no behavioral response whatever. Thus to a dog many of the objects in a room are behaviorally neutral—the pictures on the wall, the pattern of the carpet, and, in general, all objects that do not bear some functional relation to its needs and desires.

We are so accustomed to perceiving a vast number of discrete, easily discriminable objects in our own behavioral environment or perceptual field that we are

apt to assume without thinking that the world appears to a dog in a similar highly articulated and meaningful form. We forget that a dog's interests are vastly more restricted and severely practical; it perceives (i.e. responds to) mainly such classes of objects or events as are of functional importance to it, bear some relation to its needs and "interest," and these objects and events are limited in number and kind as compared with those that possess valence in our more complex perceptual world, which is the expression of our more varied and more extensive interests, both practical and contemplative. We should not expect a dog to discriminate and attend to books, or chairs, or tables, as such, but only to them as functional objects—as chewable things, or things that may be sat on or walked upon.

Objects possessing valence for the dog are, for instance, the fire or the stove before which it may lie, its cushion and its bed, the chairs on which it is or is not allowed to sit, the table which is forbidden but on which food may be found, the door by which exit may be made, the window through which it may look out, and so on. Small and insignificant objects or events may have a high valence, as for example the rustling of a paper bag, which for Gina "means" biscuits or sweets or potato-crisps, and elicits immediate attention. For many dogs, crumpled paper lying in the road has high positive valence and is investigated as possibly containing food. One dog which we had used to investigate all parcels brought into the house, nibbling a bit off the corner of each to find out what was inside—parcels had an acquired positive valence for him, through his often finding food therein. In a house in which we lived previously, the click of the latch on the garden door had high valence for

Gina and brought her racing towards it, in order to escape into the road.

In these cases, we are dealing with objects or happenings which have acquired valence through the animal's experience. But the same principle appears in unlearned or instinctive behavior. Thus, to take only one example, to a hermit-crab robbed of its "house" any small rounded movable object has positive valence and is closely investigated, and especially any hole or crevice in it, any possible opening into which the hermit crab may insert its tail (Hertz, 1933).

It should be a primary task in the study of any animal's behavior to find out what objects or events possess valence, whether positive valence inducing approach, or negative valence determining avoidance. It is, from a psychobiological point of view, far more important to draw up a table of valences than to investigate the reaction of the animal to simple physico-chemical stimuli, many of which are behaviorally neutral. The study of simple stimulus-response relations may yield physiological knowledge of value, but it hardly seems an adequate method for attacking the real problems of behavior.

#### "TRANSFER OF TRAINING"

If a certain range of things has a common functional quality or valence, one might expect that the dog would manifest similar behavior with respect to them, and would not *in practice* distinguish between them, though they might appear to the dog different in certain respects. We have seen this to be the case in Gina's response to several classes of equi-valent objects.

I am inclined to think that a similar explanation may be valid for at least some cases of so-called "transfer of training." This is strongly suggested by some simple experiments in which Gina learned to nose

up food or a ball. The first experiments were carried out on the evening of 5.11.34. The box in which Gina's best ball is kept was used for the sixteen tests, lasting 1-5 minutes each, then carried out. It was familiar to Gina by sight, but never before played with. It is a casket-shaped wooden box, of a dark brown color, 15 cm. high, 21 cm. long, 10 cm. wide; the lid projects slightly, measuring 11.7 cm. by 23 cm. In each test Gina was shown a piece of biscuit, or cheese, or a ball, which was then placed in the box and the lid closed. Though she was keenly intent on the box and occasionally pushed at it with her nose or clawed it, she did not succeed in opening it that evening. That the box had acquired "means-to-food" valence was clearly shown by the occurrence of a special behavior trait, consisting in biting my foot if it approached the box. This response is always given by Gina when food is thrown down for her; often she will not begin to eat until the ritual of biting the advancing foot is gone through. Her failure that evening I put down mainly to her expectation that I would open the box for her, as I do when I give her the ball; she often lay beside it, looked up at me, and whined. The fact that she was not allowed to seize the food or the ball when they were shown her prior to being placed in the box seemed also to invest them with a "forbidden" character.

The tests were resumed on the following evening—this time with a cardboard file-box laid on its side with the lid uppermost. It measured 15.5 by 5.2 by 24 cm., and the lid did not project; it was mottled red and brown in color. She succeeded at once in the first test, failed in the next three, obviously waiting for me to open the case, then succeeded with ease in the next four tests, lifting the lid by pushing it up with her nose. In the next test,

the ninth that evening, she was given the original wooden box, which she opened in 12 seconds. "Transfer of training" was immediate and complete.

Next morning she opened the file-box without hesitation on several occasions. In the evening she opened both file-case and box after some delay, due to starting on the hinge. She had no clear perception of the difference between the hinge and the edge of the lid. After a few more successful trials on 8.11.34, no further experiments were made until 4.1.35, about eight weeks later. She then opened the box rapidly, though she tried the hinge first; there was complete retention of learning.

On 7.1.35 an interesting experiment was carried out by chance. I had laid on the floor alongside my chair the open drawer of a wooden file-cabinet which I was using, full of papers. Gina immediately paid attention to it, inspecting its contents closely and standing up on her hind legs for it when I lifted it off the floor. It had evidently some valence for her, like the box and the file-case. On the same evening she opened at once the lid of a large red file-case which she had not previously seen.

These experiments are of course somewhat crude and incomplete but they do show clearly that at least two or three "box-objects" were functionally equivalent, as possible food containers. Gina did not *in practice* discriminate between the box and the file-cases, but fastened on the essential functional property they had in common, namely their openableness as a step towards acquiring food or a ball, both objects of high valence.

As is well known, a single painful experience may be sufficient to give a child or an animal an aversion not only from the specific object which has caused it, but also from all other similar objects. The

burnt child dreads the fire—all fires. When Gina, leaping unawares out of a hedge, was bowled over by a motor van, being slightly hurt and thoroughly scared, not only this van, but motor vehicles in general (even when stationary) became for some months objects of aversion, acquired strong negative valence. Obviously Gina did not perceive *this* motor van as such, as we should do, but merely as a large, moving, noisy and smelly thing, which one experience endowed with a pain or danger valence. Other objects with similar characteristics subsequently encountered were not in practice distinguished from the original one and were accordingly perceived as dangerous and avoided. There was, it seems, a practical generalization on the basis of a few (to the dog) outstanding characteristics. It should be mentioned, however, that the driver of the van, who was already known to Gina, and came to see if she was hurt, acquired in her eyes for some time, as an individual, a negative valence.

#### ON VALENCE, CHANGE OF VALENCE AND EQUI-VALENCE

It will be obvious to the professional student that the interpretations offered above of Gina's behavior are related in many respects to the views of Lewin, Tolman and Klüver, and that the general point of view adopted is very similar to that of J. von Uexküll, for we have been dealing with the dog's "Umwelt," or perceptual world, or behavioral environment, or phenomenal field, to use the various expressions that have been coined for the purpose. I take this opportunity of expressing my indebtedness to all these authors, and particularly to J. von Uexküll, who, though he does not use the word "valence," deals in his latest book (1934) with the perceptual worlds of animals in a manner very sim-

ilar to that adopted here. His "Merkmale" and "Wirkmale" correspond closely with "valences," and what he calls the "Wirkton" of an object is exactly what I mean by "functional valence." (I have myself been advocating since 1924 the same essential point that an animal's behavior is to be interpreted with reference to its own perceptual world.)

In the dog's perceptual world certain objects and events stand out, as we may judge from the fact that they are attended to, or sought for, that they elicit behavior. Such objects and events I have here proposed to call *valent*, or possessing *valence*. The word valence is borrowed from Lewin (1931) (See also the translators' note on p. 77 of Lewin, 1935), being the accepted translation of his expression "Aufforderungscharakter," but the use here proposed is perhaps an extension of Lewin's usage, though the basic meaning remains the same.

One might instead of "valence" use the words "meaning" or "significance," and I have above sometimes used the expression "functional significance" or "functional value" to designate one kind of valence. But there is a distinct advantage in using a neutral or technical word like valence, for it is by no means certain that the animal is aware of the significance or meaning of the valent objects or events in respect of which it shows behavior. This may well be so in cases of learning but it seems improbable in many cases of instinctive behavior, especially of the lower animals. Thus the fish-leech *Piscicola* responds to any source of water-vibration, not too far away, by directing its anterior end towards it. This may lead to its *fixing itself on a fish*, and water-vibration might accordingly be called a sign-stimulus, "meaning" the approach of a possible host. But we have no warrant in the behavior of *Piscicola* for

assuming that it is aware of the meaning of the stimulus; all we know is that in certain conditions it responds in a particular way to this particular kind of event in its environment, and that sometimes this response leads to the specific end-state or completion of the response, namely attachment to a suitable host. The fact that the response is adaptive does not justify us in concluding that it is purposive, in the sense of implying foresight of the end or goal. It is better then simply to say that water-disturbance possesses valence for *Piscicola*, instead of calling it a sign-stimulus or significant stimulus. Whether or not my generalized use of the word corresponds with Lewin's original use, we agree on the essential point namely that valence is relative to the animal's momentary state (or nascent tendency); it is not a quality of the object or event *per se*. This is strongly emphasized by Lewin, who writes:

The valence of an object usually derives from the fact that the object is a means to the satisfaction of a need, or has indirectly something to do with the satisfaction of a need. The kind (sign) and strength of the valence of an object or event . . . depends directly upon the momentary condition of the needs of the individual concerned; the valence of environmental objects and the needs of the individual are correlative (1935, p. 78).

Valence is, however, dependent not only on need, but also upon what one may best describe as "interest" or "nascent intention." Thus Gina is diverted from the ball game to a vole hunt, not by need of food, but by interest in the chase. (She does not eat the voles she catches.) The vole area has an acquired positive valence, which arouses her attention and interest, and induces her to search in it.

The fact that valence is relative to needs, or interest, indicates that it is to be considered as a quality of the animal's own perceptual or phenomenal world. This

being accepted, it is easier to understand how one and the same object in *our* perceptual world may have several different valences in an animal's world, changing from one to another according to the animal's needs and "intentions." A striking illustration of this fact is afforded by the observations of Brock (1927) on the "Umwelt" of the hermit crab *Pagurus arrosor*.

To be in a state of behavioral equilibrium with its environment *Pagurus* requires (1) a gastropod shell into which it can insert its abdomen and carry round with it as a mobile house, (2) one or more specimens of the sea-anemone *Sagartia parasitica* planted on its shell, (3) a supply of food. If any one of these necessary requirements is absent the *Pagurus* takes steps to make good the deficiency. Thus if the anemones are all removed from the house of a well fed *Pagurus* it will search round, and finding a *Sagartia* tap it and stroke it to induce it to lose tonus and slacken its hold on the bottom; it will then swing it up and press it against the shell until it adheres. The *Sagartia* has in this case its normal valence as "something to be placed on the shell." If, however, a *Pagurus*, which has been long deprived of food, but possesses a shell, well covered with anemones, is given a *Sagartia*, it will strip pieces off it and eat them. The *Sagartia* has lost its normal valence and is treated as having food valence. Finally, a well fed *Pagurus* lacking a shell, treats any free lying *Sagartia* as a possible substitute house, trying to press its abdomen into the hollow of the pedal disc. Here the anemone has house valence. Thus one and the same object, as it appears in our perpetual world, may have three different valences according to the dominant need of the animal perceiving it.

It can be shown by analysis of the extensive observations and experiments of Brock that *Sagartia* does not exist for *Pagurus* as a specific and individualized object, but simply as the bearer of certain perceptible characteristics, some of which make it a suitable object to place on the shell, others a food object, and another still a (rather ineffectual) house object. According to the dominant need, so does the attention of the *Pagurus* become directed to the characteristics of *Sagartia* that are relevant in connection with the satisfaction of the need, that are valent in the particular situation. Other objects showing some of the same characteristics may also be treated as having similar valence (see Russell, 1935).

In a small way, we have seen the same phenomenon of change of valence in considering Gina's behavior. Thus for Gina a cork may have ball valence or "means-to-cheese" valence; a dry bone may be treated as a ball or as a fantasy pup. The last example suggests an interesting parallel in the behavior of the child with reference to its toys. As Lewin says, "Exactly the same physical object may have quite different sorts of psychological existence for different children and for the same child in different situations. A wooden cube may be at one time a missile, again a building block, and a third time a locomotive" (1935, p. 76). In all cases it is the need or the interest of the animal that determines what objects, or which characters of objects, shall have valence, and what kind of valence.

In our definition of valence nothing is asserted about the *kind* of objects and events that may be expected to possess valence, but if valence is relative to needs and interest it follows that valent objects and events will in general be such as have relevance to the animal's normal behavior in maintaining its existence, in assuring its development, in reproducing its kind. They will accordingly have, as a rule, functional or biological significance (though the animal need not be aware of their biological significance).

Valent objects and events are classi-



fiable according to needs or "interests" or "desires"—in practice, however, by the type of behavior they elicit. Thus we may distinguish objects and events having food or feeding valence, water or drinking valence, danger or flight valence, foothold valence, play valence, and so on. They can be grouped in two main classes—positive valences and negative valences—according as they induce approach or avoidance. Objects may have a specific means valence, as a step towards reaching some particular end-state or satisfaction; for example, pennies and other small objects have for Gina means valence in relation to the eventual possession of an object of high food valence, namely cheese. In a biological sense, food objects also are means towards an end-state, the restoration of depleted biochemical resources, but they have psychologically an immediate value of their own, as satisfying hunger. Means objects in the limited sense have on the contrary no immediate value as satisfying a need—Gina does not eat her penny.

It is convenient to refer here to some of Tolman's views and concepts which receive support and illustration from my observations on Gina.

Tolman distinguishes as an important factor of the psychobiological field what he calls *manipulanda* qualities. "By manipulanda" he writes, "I would understand those properties of objects which actually support (i.e. make possible) *motor* manipulations. . . . Graspableness, pick-upableness, throwableness, heaviness (i.e. 'heave-ableness') and the like—these are manipulanda" (1933, pp. 397-98). Gina's balls and ball-substitutes, which are characterized essentially by pick-upableness and eventual retrievableness, are excellent examples of objects possessing manipulanda qualities. And, as we have seen, many objects stand out in Gina's

perceptual field because of what she can do about them—warm places to lie in, chairs to sit in, objects to tear up and destroy (when she was a pup). These are objects and places having *functional* valence. So for the child, as Lewin points out, many objects acquire valence by reason of their "*functional possibilities* (the Wirkwelt in von Uexküll's sense). The stairs are something that one can (or cannot yet) go up or down, or something that one climbed yesterday for the first time" (1935, p. 77). Even more important than manipulanda qualities in Tolman's view are the means-end-relations existing in the perceptual field.

"By means-end-relations" he writes, "I wish to designate those interrelational properties between environmental objects, whereby the 'enjoyment of' (i.e. the 'commerce with') the discriminanda and manipulanda constitutive of one such object will (or will not) actually lead on to an immediate possibility of 'enjoyment of' (commerce with) the discriminanda and manipulanda of such and such other environmental objects" (1933, p. 401).

The intermediate or means object is called by Tolman a sign-object, leading on to the signified object or "significate." This relationship is well exemplified in Gina's penny game, where the coin or other equi-valent object is the sign object and cheese the significate. In our suggested terminology the coin has "means" valence in relation to the food valence of the cheese.

In conclusion, a few words on equi-valence. It is to Klüver (1933) that we owe the first thorough study of this important phenomenon. In his well known investigations of the behavior of monkeys much attention was given to determining to what extent a particular "stimulus" or stimulus-pair could be changed without altering the character of the response. Thus after training a monkey to pull in the lighter (or the heavier) of two boxes

of definite weight, he found that the response was given correctly to the lighter (or the heavier) of any pair of manipulable boxes which differed sufficiently in weight. Further, the original conditions of the experiment could be altered in many respects without upsetting the correct response.

"In the critical experiments" writes Klüver, "we found a large number of situations to be equivalent to the stimulus situation during training in the sense that there was no disturbance of the response. The changes introduced in the critical situations were changes in the 'absolute' and 'relative' weight of the boxes; changes in the material and in the optical appearance of the gliding surface; changes in the pulling-in device; changes in the optical appearance of the box; changes in the distance of the boxes from the cage; changes in the distance of the boxes from each other; changes in the number of boxes; changes in the 'affective' value of the boxes" (1933, p. 59).

Other experiments with visual and auditory relata showed the same thing—a considerable range of variation was possible without altering the correctness of the response. There were of course limits to this variation, and when the limits were overstepped the altered stimuli became "non-equivalent." Klüver rightly attaches great importance to determining the "range of equivalence" of stimuli. Whereas most workers have been at pains to discover the limits of discrimination of like stimuli, it was Klüver's aim in these experiments to discover to what degree dissimilarity could be pushed without upsetting the response. In doing so he has opened out a most fruitful field for research. Many extraordinary cases have been recorded of the equi-valence, so far as behavior is concerned, of the most diverse objects, and many of the so-called "aberrations" of instinct arise from these bizarre assimilations. Thus Yerkes (1915) has shown that a female monkey may cleave to her still-born babe for weeks, until nothing but a desiccated frag-

ment of skin is left. Zuckerman (1932) has observed similar behavior in female baboons, but points out that a clinging attachment to furry objects may be shown also by young baboons and by males. He quotes also an observation by Loveridge regarding a female *Cercopithecus* to whom the warm body of a dead rat was given. She took the greatest interest in the corpse, examining the fur for fleas and "nursing" it; she clung to the rat for two days, until it was green and stinking. Such cases can "in large part be explained as the operation of a response common to females of apparently all ages as well as to males, and one for which the significant stimulus can be greatly altered—from monkey baby to dead rat—without effectively altering the character of the response" (1932, p. 301).

Wiesner and Sheard (1933) have shown that the retrieving response in nursing rats may be elicited not only by their own young up to a certain stage, but by the young of other rats, by young mice, young rabbits, young kittens and young chicks. "The rat is not 'interested in' her own young because they are hers (and recognizable as such by some odor or other property) nor because they are rats, but because they are small young creatures; and any object to which these terms apply is 'her young' to the rat" (1933, p. 135). All these objects are, in our nomenclature, equi-valent with the usual object retrieved, the rat's own young.

It would be easy to adduce other instances of equi-valence, extending over a considerable range of objects. I shall content myself with making some tentative suggestions as to the possible bases of equi-valence. We have first of all such cases as are exemplified by Gina's response to motor vehicles in general, after a painful experience of one in particular. Here it is probable that the objects concerned are not

separately distinguished; they have some characters in common which have acquired a danger valence, and in the danger situation the dog ignores their differences. Many cases of instinctive response also come under this heading, where there is response, not to an individualized object, but to certain valent characteristics of it. It is well known, for example, that a fly which normally oviposits in carrion will on occasion lay its eggs on a flower that has a carrion smell. Here the decaying flesh and the flower have a common valent characteristic; the fly does not seek out carrion *qua* carrion but merely "something with a carrion smell." A careful study of the perceptual field in instinctive action would probably show that in many cases there is response, not to an individualized object, but merely to certain, quite simple, valent characteristics, which may be shown by other objects besides the normal one. This point has been very clearly brought out by Miss Smith (Mrs. Bartlett) (1923) apropos of a discussion of "aberrations" of instinct like that of the carrion fly. "In no such case," she writes, "does the animal recognize the object which prompts the instinctive action as a single, specific, individualized object; it responds rather to certain qualities, qualities which, it frequently happens, are common to many different objects, while the remaining qualities characterizing the object in question are ignored" (1923, p. 81). In other words, only certain characters or qualities of the object, as we perceive it, possess valence for the animal, the others are, so far as we can tell from the animal's behavior, simply not perceived, form no part of its perceptual world. And the valent qualities, occurring as qualities of another object (an object *to us*) may also elicit the instinctive action.

A second group of equi-valent objects

are those that can be used in the same way, which are therefore *functionally* equivalent, or possess the same or similar "manipulanda" valence. An example of this class is the group of heterogeneous objects which are used by Gina as "balls." So too a chimpanzee will use all sorts of objects as "tools" for drawing into the cage food objects which are out of arm's reach.

In a third group of equi-valences it would seem that a strong and unsatisfied need or desire may invest with valence objects which would not normally possess valence or come into the picture at all. We know that valence is relative to needs; it is understandable therefore that, where the need is imperative, behavior in attempted satisfaction of it may bring into its ambit objects which normally would be neutral or might even possess negative valence. A case in point is afforded by the incubating behavior of the Emperor Penguin (*Aptenodytes forsteri*). This bird nests in the middle of the Antarctic winter, and so strong is its "drive" to incubate its eggs that it will continue to sit on frozen eggs. "Indeed, in their desire for something to hatch, some who had been deprived of their eggs were seen to be attempting to incubate pieces of ice, and, unlike Adélies, they seem ever ready to snatch and foster the young of their neighbors" (Levick, 1914, p. 136). They will also carry about and nurse frozen and lifeless chicks until the down is worn away.

Yet a fourth category of valence is required to cover cases where a "fantasy" value is attributed to more or less neutral objects. Thus a child may use a wooden cube to represent or stand for a railway engine, or a set of marbles to represent a company of soldiers. I can see no other explanation of Gina's temporary adoption of a bone than to assume that it was to her

a substitutionary or fantasy pup. In such cases a valence is conferred on the object that has no real warrant in the perceptible characteristics of the object.

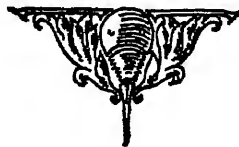
But we must leave the subject of equivalence here. It is one of immense importance and deserves far more study and research than it has yet received. It will show more clearly than any other line of study the real value, and indeed the in-

dispensability, of the hypothesis that an animal's behavior must be interpreted with reference to its own perceptual world, its own "Umwelt."

I have been concerned in this paper mainly to show how the almost casual study of a very ordinary dog contributes to the support and elaboration of some important modern views in animal psychology.

#### LIST OF LITERATURE

- BROCK, F. 1917. Das Verhalten des Einsiedlerkrebses *Pagurus arator*. *Roux's Archiv.* vol. 112, pp. 204-38.
- HERTZ, M. 1933. Über das Verhalten des Einsiedlerkrebses *Gibbanarius misanthropus* gegenüber verschiedenen Gehäuseformen. *Zst. vergl. Physiol.*, vol. 18, pp. 597-621.
- HOBHOUSE, L. T. 1926. Mind in Evolution. *London*. (Earlier editions, 1901, 1915).
- JENNINGS, H. S. 1915. Behavior of the Lower Organisms. *New York*. (First edition, 1906.)
- KLÜVER, H. 1933. Behavior Mechanisms in Monkeys. *Chicago*.
- LEVICK, G. MURRAY. 1914. Antarctic Penguins. A Study of their Social Habits. *London*.
- LEWIN, K. 1931. Environmental forces in child behavior and development. In: A Handbook of Child Psychology. *Worcester*.
- . 1935. A Dynamic Theory of Personality. (Selected papers, trans. D. K. Adams and K. E. Zener). *New York and London*.
- MCDUGALL, W. 1923. An Outline of Psychology. *London*.
- PITT, F. 1927. Animal Mind. *London*.
- RUSSELL, E. S. 1924. The Study of Living Things. *London*.
- . 1934. The Behaviour of Animals. *London*.
- . 1935. Valence and Attention in Animal Behaviour. *Acta Biotheoretica*, vol. 1, pp. 91-99.
- SMITH, E. M. 1923. The Investigation of Mind in Animals. *Cambridge*. (First edition, 1915).
- STOUT, G. F. 1913. A Manual of Psychology. *London*.
- TOLMAN, E. C. 1932. Purposive Behavior in Animals and Man. *New York and London*.
- . 1933. Gestalt and sign-gestalt. *Psychol. Rev.*, vol. 40, pp. 391-411.
- URKÜLL, J. VON. 1921. Umwelt und Innenwelt der Tiere. *Berlin*.
- . 1926. Theoretical Biology. *London*.
- . 1934. Streifzüge durch die Umwelten von Tieren und Menschen. *Berlin*.
- WISNER, B. P., and SHEARD, N. M. 1933. Maternal Behaviour in the Rat. *Edinburgh and London*.
- YERKES, R. M. 1915. Maternal instinct in a monkey. *J. Anim. Behav.*, vol. 5, pp. 403-05.
- ZUCKERMAN, S. 1932. The Social Life of Monkeys and Apes. *London*.





# WHITEHEAD'S PHILOSOPHY OF ORGANISM

## AN INTRODUCTION FOR BIOLOGISTS

By W. E. AGAR

*Professor of Zoology, The University of Melbourne*

### INTRODUCTION

THE concept of Organism is one which is very much to the forefront among philosophical biologists at the present time, and it appears in contemporary psychology in the doctrine of Gestalt. Whitehead is frequently invoked as an advocate of Organism, but it must be doubted whether many biologists are fully acquainted with his views, which indeed belong more to the domain of philosophy than of science. Nevertheless it must surely be of great importance to biologists who desire to work with any conception of Organism to know what an acknowledged great thinker, both in metaphysics and mathematics, believes to be involved in the concept of parts united into an organic whole—that is to say, a whole which has a unity of its own which cannot be expressed simply as a summation of its parts. This involves, for Whitehead, a discussion of the nature of reality; and, indeed, the nature of organisms, in the sense in which that word is commonly used by biologists, occupies only a minor part of his discussions.

Unfortunately, Whitehead's exposition must prove extremely difficult to anyone not well read in metaphysics, and accustomed to the modes of reasoning of philosophers, and he rarely helps the reader by application to a specific example. The following is an attempt to give a descriptive outline of his system for biologists who desire to learn something of the general nature and scope of this oft quoted

theory of Organism. The writer is quite incompetent to discuss the metaphysical questions involved, and he has of necessity passed over many of them without even mention. The reader must therefore constantly bear in mind that any lack of conviction in the reality of Whitehead's system which he may feel in reading this account should be ascribed to the crude way in which it is presented, and especially to the almost complete absence of any indication of the reasoning lying behind Whitehead's conclusions. Moreover, the reader should realize that this is not merely a summary, but also an interpretation, and an interpretation may be misleading. Many of the specific applications are the present writer's. For all these reasons, this account should be taken, not as a sufficient indication of Whitehead's philosophy, but as an introduction to the study of his own works.

Whitehead's philosophy, so far as we are concerned with it, is set out in the trilogy, *Science and the Modern World*, 1926 (referred to in the following pages as *S.M.W.*), *Process and Reality*, 1929 (*P.R.*) and *Adventures of Ideas*, 1933 (*A.I.*). Of these, *Process and Reality* stands out as containing the complete system. In fact, although Whitehead says that each book may be read separately, the present writer found *Science and the Modern World* unintelligible in regard to many fundamental issues when taken by itself. Chapters XI-XV of *Adventures of Ideas* contain a general account of the main ideas involved. But *Process and Reality* contains the system set

out as a whole, and in detail, the other books being chiefly helpful in giving the student a general orientation.

The student of Whitehead will find Dorothy M. Emmet's book *Whitehead's Philosophy of Organism* a most valuable commentary on *Process and Reality*.

### *Reality as process*

Whitehead develops his system primarily from consideration of conscious human experience—and at the other end of the scale, from the conclusions of mathematical physics. "Any doctrine which refuses to place human experience outside nature, must find in description of human experience factors which also enter into the descriptions of less specialized natural occurrences." (*A.I.* 237)

Reality is thus conceived as a process of experience (only rarely of the conscious order). Both introspection, and physics, tell us that this process is not continuous, but atomic. An electron is a vibratory series of experiences; human experience is also a succession of atomic processes of experience, each lasting in this case perhaps about  $\frac{1}{10}$  to  $\frac{1}{2}$  a second (the "specious present"). Each moment of experience is a transition between two worlds, the immediate past and the immediate future. But as human experience, e.g. a train of conscious thought, tells us, the past still lives in the present, and the present acts into the future. Whitehead's system deals primarily with the nature of the atom of process (of experience) itself, and with the relation between atoms of process, especially between a given atom of process and its immediate predecessors and successors. That is to say, how the past is immanent in the present, and this acts into the future.

Accordingly, the essence of a thing is not what it is, or where it is, but what it does. How it receives the past into its

own constitution, and transmits itself to the future—its "objective immortality."

In order to understand Whitehead's system it is necessary from the outset to hold steadily in view this notion of reality consisting in process and not in substance. This is consistent with the physical analysis of a lump of matter into a collection of ultimate processes (such as electronic vibrations). A single one of these processes, if it be incapable of further analysis, is the physical aspect of an "actual entity." (Cf. *S.M.W.* 190–198). The present writer, who has but a superficial knowledge of physics, must be content to quote Bavinck in this connection. (*The Anatomy of Modern Science*, 1932, p. 199.)

... wave and oscillation in themselves have no other meaning in modern physics than periodic changes of some quantity, no matter of what kind. When now everything that can be stated regarding the processes in question depends only on the form of these processes, while the nature of the quantity itself which changes according to the wave formula has become a matter of complete indifference, then all that plays any part in physics is the process itself, and it does not in the least matter what the something is in which the process takes place. . . . This fundamental idea needs only to be carried to its logical conclusion for us to see that a final state of physics is not merely imaginable but already very nearly reached, in which the notion of a substance is no longer made use of, since everything which can be stated physically is founded upon the law of the processes.

Reality, then, consists in *process*, not in substance supporting qualities. The final real things of which the world is made up are "*actual entities*," which Whitehead also calls "*actual occasions*" to emphasize the fact that they are atoms of process and not of substance. The two terms, entity and occasion, are therefore synonymous.

Although experience is atomic, the atoms (actual entities) can be analysed into parts when considered as objects, but as experiencing subjects they are indivisible wholes.

The word *process* refers to the process of

becoming, or self-formation, of actual entities. An actual entity is a "drop of experience" (*P.R.*, 25). Experience, or feeling, implies both a subject which feels and an object which is felt. The object felt (in Whitehead's system) is a complex of feelings, originating as feelings transmitted to the present actual entity by previous entities whose own feelings originated in the same way. "An actual entity is . . . . an individualized feeling. . . . Its feeling is its whole nature, in which it becomes and perishes." (Emmet, 181).

The conception that the world, including the physical world, is composed of entities which are "drops of experience" or feelings will seem to many people a strange one. But Whitehead does not use the term "feeling" in the sense of conscious feelings. Even "conceptual feelings" very seldom have the conscious form. Energy in the language of physics corresponds with emotional intensity in Whitehead's language. The wave lengths and vibrations of physics are "pulses of emotion." A quantum of energy is possibly a single actual entity. "Physical science is the science investigating spatio-temporal and quantitative characteristics of simple physical feelings" (*P.R.*, 337). To quote Emmet again (p. 142) "We must bear in mind that 'feeling' is here used throughout as the purely general term for any kind of acting or being acted upon, in such a way that the make-up of the subject is affected." It is essential that the reader should understand the word "feeling" in this sense wherever it occurs.

#### THE LIFE HISTORY OF AN ACTUAL ENTITY

We will start by attempting to sketch out the life history of a simple actual entity. This life history consists of three essential phases:

(1) The initial phase, in which the general nature of the atom of experience constituting the actual entity is determined by its relation to the preceding actual entities (the responsive phase). For instance, the actual entity which arises at the space-time location at which the period of a light wave has just completed itself, has itself the nature of a similar period. The actual entity arising at the location where a phase in a stream of conscious thought (occupying the duration known to psychologists as the specious present) has just completed itself, tends to continue the stream of thought.

(2) A final phase in which the actual entity faces the future as itself an agent determining the character of new actual entities (the phase of satisfaction).

(3) In the higher types of actual entities, these two phases are connected by a complex phase called the supplemental phase, the term indicating the mental activity, with a measure of freedom, concerned in this stage. In the simpler types of actual entities—as found in inorganic bodies—this phase is negligible (though never completely absent) i.e. the initial phase passes over quickly and almost determinately into the final phase.

Let us now take in more detail the life history of a simple actual entity—one for instance forming a component of an inanimate material object. We at once meet the difficulty that we cannot easily fix on a particular class of entity to use as a sample. For individual actual entities (except those in the stream constituting our own conscious processes) are not available for inspection. Not only is there the logical difficulty that we cannot know anything about the internal processes of an actual entity except by inference, and by analogy with our own conscious processes, but even as physical objects they escape direct inspection. For exceedingly short

temporal durations (e.g. the period of a light vibration) and minute extensions of space are concerned. Anything big enough, and lasting long enough, to be perceived consists of a vast number of actual entities, just as they consist of a vast number of atoms, electrons, etc. Even electrons are probably not the limit of physical simplicity—that is to say, consisting, at any one moment, of a single entity. But for the sake of example, “an electron” may be conceived as consisting of a stream of electronic entities or occasions, each occupying an exceedingly short temporal duration.

An actual entity or occasion occupies an atomic duration (time being the succession of atomic durations) which however may be of very different extent for different entities. It is also located in space, in the sense that it has a regional standpoint from which its prehensions are made and its own causal influence extends.

#### *Subjective aim*

As we have seen, its real nature is an atom or act of experience. At its moment of origin its only specific characterization is its *subjective aim* (or end-in-view) and its corresponding *subjective form*. The nature of these depends upon the location of the nascent actual entity in the *extensive continuum* (described below: the most prominent feature of the extensive continuum is its space-time aspect). In general, the subjective aim and form of the nascent entity are determined by, or taken over from, the actual entity which has just completed its life history, and added itself to the general *creativity*, at that point of space and in the immediately preceding temporal duration (the Doctrine of the Conformation of Feeling, *A.I.*, 235). The life history of the actual entity is essentially the fulfilment of its subject aim.

The notions of creativity and subjective aim will be amplified later.

#### *Initial data and objective datum*

The just nascent actual entity is therefore a feeling or atom of experience with a subjective aim conformable with that of its contiguous predecessor or group (nexus) of predecessors. But experience needs something (objects) to experience. These are also provided by its contiguous predecessors, and through them, by the actual entities of its whole preceding world, as will be seen later. These constitute the *initial data* (for feeling) of the nascent actual entity, and they, or rather, aspects of them enter into the constitution of the new entity to form the *objective datum* for the new actual entity. They have been *objectified* in the new entity, which on its part is said to have *prehended* them, or received them into its own constitution. An aspect of an actual entity means “a feeling entertained by an actual entity” (Cf. *P.R.*, 334).

The difference between the plural and singular forms of the terms initial data and objective datum is significant. The initial data present a multiplicity of feelings “to be felt” by the new actual entity. The objective datum which is actually felt is a unity formed by the *concrescence* of the originally separate feelings. (*P.R.*, 312).

(This concrescence into an objective datum of the feelings provided by the initial data is illustrated in perception, which is a complicated form of conscious prehension. We see objects as wholes, not as a mere multiplicity of the parts composing them.)

#### *Prehension*

The idea of prehension is fundamental for Whitehead's system. His simplest characterization of it is as follows:



A prehension involves three factors. There is the occasion of experience within which the prehension is a detail of activity; there is the datum whose relevance provokes the origination of this prehension; this datum is the prehended object; there is the subjective form, which is the affective tone determining the effectiveness of that prehension in that occasion of experience (*A.I.*, 227).

The contribution of the various actual entities in the initial data to the general character of the objective datum will of course vary greatly, and depends partly upon relevance to the subjective aim. (In perception, again, we perceive our environment in its relevance to our activities.)

The feelings transmitted to the nascent actual entity by the initial data are *physical feelings*, and objectification is the reproduction in a succeeding actual entity of a feeling in a preceding actual entity. This is the *efficient causation* of science, subjective aim being *final causation*. It expresses the effect of one thing upon another. "A simple physical feeling is an act of causation. The actual entity which is the initial datum is the 'cause', the simple physical feeling is the 'effect'" (*P.R.*, 334). The notion of cause in Whitehead's philosophy will be taken up again later.

#### *Eternal objects*

But we have to remember that the actual entity is an experiencing subject, with a subjective aim at a specific form of self-realization. Certain external feelings have been appropriated into its constitution, and now constitute its own physical feelings. How is the actual entity going to utilize these for its self-realization? This "how" involves the *conceptual feelings of eternal objects*.

We must now consider the nature of these eternal objects—a strange-sounding term to the layman. Eternal objects determine *how* the external world enters

into the constitution of a new actual entity via its feelings (*P.R.*, 207). They are "forms of definiteness," an expression which has great significance in Whitehead's system. Actual entities and eternal objects are alike entities. But an entity is *actual* only when it is self-realizing. An eternal object, though an entity, is not an "actual entity," because it only functions in the self-creation of an actual entity, not in its own self-creation (*P.R.*, 34).

This function is expressed by saying that the eternal object has *ingression* into the actual entity. The actual entity itself prehends the eternal object, just as it prehends its initial data.

To most scientists, the existential status of the eternal objects will probably not be at all clear, and the conception, and the language in which it is expressed, may even be repugnant to that vast majority of scientists who are not in a position to appreciate the metaphysical reasoning which led Whitehead to adopt it. But it is enough for our purposes that the idea expresses the notion that the possibilities of self-realization of actual entities from their initial data are not infinite; in other words, that the possible ways in which the initial data can enter into the constitution of new entities as their objective data are specific and limited, and that these possibilities are named by Whitehead, eternal objects. "The essential point in this view of nature is to show that, while events come to pass and perish, their flux sustains permanent and recognisable characters, which make possible sense-perception and natural science" (*Emmet*, 113). Eternal objects are therefore universals, qualities, etc. The ideas of hardness, motion, man, drunkenness, are eternal objects (*Cf. P.R.*, 72).

Consider our perception of a stone. Every different stone will produce a

slightly different objective datum for the percipient actual entity in the brain. If it were not for these forms of definiteness there could be no perception of stones as such. The idea of a stone would not exist. Not only would all objects which we know as stones be perceived as unique objects (without the common quality of stoniness), but an individual stone would be perceived as a different unique object on every occasion of perception, since it would practically never happen that the conditions of the perceiver, the stone, and the perspective from which it was perceived, were identical in two acts of perception.

But perception is a conscious form of prehension, and similar considerations can be applied throughout the whole order of nature. Without these "forms of definiteness" there could be no *classes* of objects (such as atoms, men) at all. Since every actual entity must have initial data different from that of every other actual entity, and apprehend them from a unique perspective, no two actual entities would ever complete their processes in the same way were it not for the limitation of possibilities imposed by the eternal objects.

A physical feeling is a feeling of an actual entity (in the initial data). It is a merely passive being acted upon by another actual entity (Emmet, 147). The feeling of an eternal object is a conceptual feeling because it belongs to the new actual entity in its capacity of a responding subject. In perception, physical feelings may be compared with the reception of the stimulus, the eternal object characterizing the objective datum is the percept—e.g., the stone.

The subjective form of a conceptual feeling of an eternal object has the character of a valuation of that eternal object—i.e. its value for the realization of the subjective aim of the actual entity. This (prin-

cipally in the higher types of actual entities) will determine whether it is to be allowed to enter into the concrescence of feelings which is the developing actual entity.

To return to the life history of our simple actual entity—say, an electronic occasion. The overwhelmingly dominant feeling in its objective datum is the objectified preceding electronic occasion or entity (which also determined the subjective aim of the present actual entity). But this preceding electronic occasion was similarly conditioned by the electronic occasion before that, and so on. The eternal object correlate to the physical feelings of the nascent electronic occasion we are now considering, will therefore be the same as for the preceding one. "From each physical feeling there is the derivation of a purely conceptual feeling whose datum is the eternal object determinant of the definiteness of the actual entity, or of the nexus, physically felt" (*P.R.*, 36). This is the category of Conceptual Reproduction (*P.R.*, 141). In this instance, therefore, the eternal object is necessarily appropriate to the subjective aim, and the conceptual feeling of it is received into the concrescence.

The life history of the actual entity is now nearly over. It attains *satisfaction* of its subjective aim through concrescence of the physical and conceptual feelings into one final, determinate, definite, feeling. The completed actual entity is a feeling which has felt feelings—and the final stage of that feeling (its satisfaction) is necessarily bound up with the sort of feelings it has felt. The genesis of this final determinate feeling out of the feelings felt (which are at once objects and creative agents) and the feeling which feels (subject) is the process of concrescence. The actual entity has, so to speak, made up its mind out of the data presented to it,

and is now about to act as creative agent itself. The completion of the period of one electronic vibration initiates the next.

In such a case as this, each actual entity will re-enact the character of the preceding one, for (i) the subjective aim and form of the nascent actual entity is determined by its space-time contiguity to the immediately preceding electronic actual entity, or occasion, (ii) the overwhelmingly most important physical feelings of its initial phase are the objectified feelings of this preceding electronic occasion, (iii) consequently, the eternal object of the conceptual feeling is the same as in the previous occasion, and also appropriate to the fulfilment of its subjective aim.

#### *Enduring objects*

The sequence of such electronic occasions together form the *enduring object* which we call "an" electron, and this will persist until some other actual entity—say, some energy wave—enters into the initial data in such a way as to alter the character of the objective datum.

In the case of more complex actual entities, such as those in living organisms, the physical and conceptual feelings available for the concrescence are much more complex. Before considering the life history of such an actual entity, however, we must consider more closely a number of conceptions which are essential to Whitehead's philosophy.

#### *Objective immortality*

With the achievement of the final determinate feeling—the satisfaction—the life history of an actual entity is over, for its subjective aim, or final cause, no longer operates. It perishes, but has *objective immortality*, in that it enters into, and is a determinant of, other actual entities. Indeed, it is cardinal to Whitehead's philosophy that the subjective aim of an

actual entity is not merely at self-realization, but at self-realization as an agent creative of other entities like itself, or at least of the production in other actual entities of feelings like its own. Satisfaction has a *superjective* character, in its function as a determinant of other entities like itself. Whitehead speaks of this superjective character as *physical purpose* (*P.R.*, 392).

Creative emphasis, or causal efficacy, is dependent upon unity or order in the creative agent. It is therefore basic to the nature of actual entities that their subjective aim is to unify the multiplicity of their physical and conceptual feelings into a single feeling. But even in the case of a completed actual entity, though its satisfaction is defined as "one complex fully determinate feeling" (*P.R.*, 35), yet when this satisfaction is objectified as datum for a succeeding entity, it is divisible, as we have seen, into its component feelings (felt by the new entity as physical feelings). "By reason of this 'divisible' character causation is the transfer of a feeling, not of a total satisfaction" (*P.R.*, 337) and again (p. 334) he states that the objective datum is a concrescence of feelings *entertained* by the actual entities which are the initial data.

#### *Physical and mental poles*

Physical feelings are the *physical pole*, and conceptual feelings the *mental pole* of the actual entity. The latter term does not, however imply consciousness, which is characteristic of only a very limited class of actual entities. Every actual entity is dipolar in this sense, though the relative importance of the two poles differs in different entities. In the simple inanimate type of actual entity which we have been considering so far, the mental pole is negligible, for there are no conceptual feelings of eternal objects beyond

those dominant in the objective datum. The electronic occasion does not have to choose between possible modes of reaction to its physical feelings, because only one is presented to it.

Hence, as we have seen, such actual entities merely reproduce the character of that portion of the initial data which was dominant in their own prehensions. "Physical endurance is the process of continuously inheriting a certain identity of character transmitted through a historical route of events" (*S.M.W.*, 159). A molecule is an enduring object in this sense, containing subsidiary strands of enduring objects (atoms), and these again further subsidiary strands, the electrons and protons. A light wave is an enduring object, the actual occasions of which are the single vibrations. Some kinds of enduring objects form material bodies, others do not (*P.R.*, 152). The continuity of human personality, of a lump of rock, and of an electron are all of the same nature. They are all enduring objects, their continuity being due to the inheritance of subjective aim and form by each actual entity from its predecessor. "Our consciousness of the self-identity pervading our life-thread of occasions is nothing other than knowledge of a special strand of unity within the general unity of nature" (*A.I.*, 241). It is an exhibition of the object-to-subject structure of experience. It can be otherwise stated as the vector structure of nature.

Some enduring objects—such as living organisms—endure, not through mere re-enactment of character from actual entity to actual entity, but by originative response, adapting the organism to changes in the environment. The mental pole is more in evidence, there is more elaborate derivation of conceptual feelings, with selective concrescence. The case of living organisms is dealt with more fully below.

The word *event* (*P.R.*, 101) used above needs explanation. An actual entity is an atomic event; the word can be used also to express any group of entities (nexus) exhibiting a certain coherence—e.g., an electron, a tree, a cricket-match. In fact, the words *nexus* and *event* may signify the same thing.

The word *nexus* expresses the "togetherness" of atomic parts. A molecule, for instance, is a nexus of atoms. Indeed, the whole universe is in one sense a nexus. Further consideration of the conception of nexus will be taken up below.

#### THE EXTENSIVE CONTINUUM

We now come to the general scheme of relatedness by which the prehensions of any one actual entity are bound together into a unity, (the process of concrescence) or by which entities are bound into *nexus* (*P.R.*, 408).

Eternal objects are *all* the possible ways in which entities or *nexus* could enter into the constitution of other entities. But not all possible ways are realizable in our own cosmic epoch. What is possible is determined by the general scheme of relatedness which obtains in our universe. This general scheme of relatedness Whitehead calls the *extensive continuum*. The character of the extensive continuum therefore imposes a limitation on possibilities of realization of eternal objects. Other cosmic epochs, with different extensive continua, would contain things exhibiting qualities and characteristics impossible in our own. For this reason Whitehead speaks of eternal objects as *pure potentials* and the extensive continuum as a *real potential*.

The most obvious feature of our own extensive continuum is its space-time character—the space-time continuum, but it has a more fundamental character than that, and includes more fundamental kinds

of relatedness. "According to the philosophy of organism, the extensive space-time continuum is the fundamental aspect of the limitation laid upon abstract potentiality by the actual world. A more complete rendering of this limited 'real' potentiality is the 'physical field' " (*P.R.*, III).

At this stage I will introduce a diagram, with apologies to Professor Whitehead for such a naïve attempt to convey the writer's notion of this part of his system. The diagram is intended merely as an aid to verbal description of the notion of the extensive continuum, (so far as its space-time quality is concerned) with contained

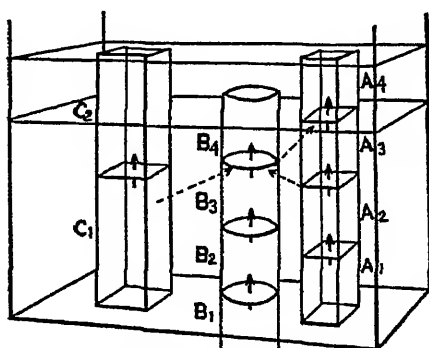


FIG. 1. FOR EXPLANATION SEE TEXT

actual entities. It obviously must not be taken as representing a model. In the diagram, three-dimensional space is represented by the two-dimensional horizontal plane, while the vertical dimension represents time, the temporal succession reading upwards. The outline of the whole figure, before the columns inside it were erected, represents the extensive continuum in its merely potential aspect—divisible, but not yet divided.

The three columns, *A*, *B*, *C*, each represent an enduring object, each compartment (*A*<sub>1</sub>, *A*<sub>2</sub>, etc.) being an actual entity. Only the uppermost entity of each column would be in existence at the moment.

Each of these enduring objects consists of a single strand of entities. Such simple enduring objects are rarely found in nature. Even an electron probably consists of several strands. An atom certainly contains many such strands (electrons, protons). But for sake of an example we can visualize *A*, *B* and *C* each as objects at the limit of simplicity of physical objects. They might also represent elements in trains of conscious thought—a reminder that the diagram is as purely symbolic as words.

The spatial dimension (any horizontal plane in the whole solid) is atomized by the actual entities. The situation of the cross-section of a column in the cross-section of the whole solid represents the position of the actual entity in space at that instant of time. The unoccupied spaces between the columns represent "empty space."

The time dimension is atomized into "epochs" or durations by the horizontal partitions between the actual entities of each column. The vertical extent of *A*<sub>2</sub>, for instance, represents the duration of the entity *A*<sub>2</sub>. The succession of durations constitutes the progress of time. Whitehead's views as to the nature of the subdivisions within a duration are not essential for present purposes.

The arrows in the diagram represent objectifications of feelings of antecedent actual entities in succeeding actual entities. For the sake of clarity in the diagram, the enduring objects are shown separated from each other, and therefore the arrows connecting actual entities of different enduring objects have to cross intervals of empty space ("action at a distance"). Whether this kind of action actually occurs or not, it is clear that the physical prehensions known to science—i.e. transmission of energy—do not normally take place in this way. An object

influences another object that is not in direct contact with it either through intermediate contiguous material objects, or by means of a wave of energy passing from one object to the other. In the latter case the influence of the object emitting a ray of light is transmitted to the object receiving it by inheritance from occasion to occasion (the individual undulations) in the ray of light. Whitehead points out that it is not necessary for his philosophy to deny that there is direct objectification of one occasion in another which is not contiguous with it. He suggests that telepathy would illustrate this latter type of objectification (*P.R.*, 435-6).

The provision of empty spaces between the enduring objects oversimplifies the situation in another way, since in nature there will normally be a group of antecedent actual entities, not merely a single one, contiguous with the new actual entity and constituting its initial data.

The temporal durations, the succession of which constitute time, are of very unequal extent. As shown in the figure, the durations of *C* are twice as long as those of *A* and *B*. *A* and *B* have durations of the same extent, but they are out of phase. The duration of an actual entity (vibratory period) in some forms of energy may be only a billionth of a second. Those constituting the stream of human consciousness (the "specious present") have much more extensive durations. Whitehead apparently allots them the limits of about  $\frac{1}{16}$  to  $\frac{1}{2}$  a second (*A.I.*, 133). Many psychologists, however, allow much wider limits. God is also an actual entity, whose duration includes the whole of time.

Events are contemporary when they arise in causal independence of each other—when, for instance, having regard to the finite velocity of light, there has not been time for causal effect to be transmit-

ted through the chain of intervening entities.

The diagram is greatly simplified by the fact that the three enduring objects are at rest with reference to one another. Actual entities themselves do not move in space any more than in time. Motion refers to the enduring object as a whole, and concerns the spatio-temporal relations of succeeding to preceding entity.

Let us now return to the life history of an actual entity. The entity begins as an atomization of the extensive continuum, by which regional standpoints are provided for the new generation of actual entities. The factor which brings about this atomization is creativity. The character of creativity is described by Emmet as follows (p. 73) . . . "it is the urge towards differentiation and unification, i.e. towards the individuation of itself into many actualities, which are called its 'creatures,' and towards the growing together of these creatures into new unities." Whitehead says "Thus God's purpose in the creative advance is the evocation of intensities" (*P.R.*, 147)—and degree of intensity is proportional to degree of coherence, or of order in unification.

The mode in which the atomization takes place depends upon the relations in the extensive continuum of the actual entities which have just completed themselves. Thus, in the diagram, the satisfaction of *A*<sub>3</sub> determines that the supervening atomization of the extensive continuum will include a regional standpoint *A*<sub>4</sub> contiguous to *A*<sub>3</sub>.

#### *Subjective form*

Perhaps the simplest way of describing the actual entity at the moment of its differentiation out of the general creativity is as a feeling with an aim at greater intensity of feeling. The particular inten-

sity or satisfaction which this entity aims at (its subjective aim) depends upon its location in the extensive continuum and also determines what aspects of the initial data will be objectified in the actual entity as its objective datum.

It is tempting to try to illustrate the notion of the subjective aim and form of a simple nascent actual entity arising in conformity with those of its principal predecessor, by reference to the diagram. The absurdity of trying to explain such an idea pictorially, as well as the play on the word "form," is too obvious for the attempt to be misleading. But let us consider the enduring objects, *A* and *B* in the figure. They will be continued by *A*<sub>8</sub> and *B*<sub>8</sub>. One can picture *A*<sub>8</sub> and *B*<sub>8</sub> at the moment of their atomization out of the extensive continuum as having the "form" of a cube and a cylinder respectively, but as yet empty of content. The conformity of the shapes of the new entities with those of their predecessors represents the conformity of the subjective aims, and therefore the subjective form of the feelings by which the forms will be filled in the process of concrescence. "The Subjective Form is the feeling of the subject, derived from its objects, and re-directed upon them" (Emmet, 160). In the simpler types of actual entities, the "form" will be "filled" automatically, for the same factors that determine the subjective aim will also supply the appropriate data for its satisfaction. But in more complex cases—especially, as we shall see, in living actual entities—this is not necessarily the case. The entity may have to manipulate its data (by selection of external objects gaining ingression into the actual entity), or the data received may cause the actual entity to modify its subjective aim and form.

Although the subjective aim is given at the moment of birth of the actual entity,

nevertheless the entity has autonomy in the modification of its initial subjective aim (*P.R.*, 347) and again, Whitehead talks about conceptual prehensions adjusting and readjusting subjective forms. "The subject completes itself during the process of concrescence by a self criticism of its own incomplete phases" (*P.R.*, 345).

#### *Efficient and final causation*

The objectification of aspects of the preceding actual world in each entity is felt by that entity as physical feelings. In the language of causation, physical feelings are efficient causation. "Efficient causation expresses the transition from actual entity to actual entity" (*P.R.*, 209). "The physical theory of the structural flow of energy has to do with the transmission of simple physical feelings from individual actuality to individual actuality" (*P.R.*, 360). Or, quoting Emmet (p. 142), "So 'causation' becomes the reproduction in one actual occasion of the feelings of another, or, more precisely, the conformity of the feelings of the present occasion to the feelings of others."

On the other hand, subjective aim is *final causation*. "Concrescence moves towards its final cause, which is its subjective aim" (*P.R.*, 298).

It appears, therefore, that in Whitehead's system causation has the "anthropomorphic" sense of agency. This is the consequence of his resolute application of the principle that man is part of the order of nature, and therefore that one must not look in nature for an order different in principle from what one finds exemplified in man. Not only final causation, but also efficient causation is ultimately referable to an agent, for the subjective aim (*final causation*) of an actual entity is not merely at self-completion, but at self-realization as a creative agent, which is

accomplished through its efficient causation of other actual entities.

#### A COMPLEX ACTUAL ENTITY

Now let us consider the life history of a more complex actual entity—such as those constituting vital processes in living organisms (metabolism, etc.) and, above all, actual entities in the brain having the conscious form.

Firstly, consider again, by way of contrast, certain features of simple actual entities.

The simplest grade of actual occasions must be conceived as experiencing a few *sensa*, with the minimum of patterned contrast. The *sensa* are then experienced emotionally, and constitute the specific feelings whose intensities sum up into the unity of satisfaction. In such occasions the process is deficient in its highest phases; the process is the slave to the datum. There is the individualizing phase of conformal feeling, but the originative phases of supplementary and conceptual feelings, are negligible (*P.R.*, 162—*sensa* are eternal objects, *P.R.*, 160).

Again, in inorganic actual occasions "the influx of objectifications of the actualities of the world as organized vehicles of feeling is responded to by a mere subjective appropriation of such elements of feeling in their received relevance" (*P.R.*, 249).

In the more complex entities the mental pole is more active—there is a richer derivation of conceptual feelings (Category of Conceptual Reversion), and a more selective concrescence.

It will be easiest to take as our example of such a complex entity, a conscious actual entity (occasion) in the human brain. Consider for instance, the perception of an object, say a fruit. First, the fruit, together with its surroundings, is prehended by the actual occasions constituting the retina of the eye at the moment, in the form of feelings inherited from occasion to occasion constituting the periods of the light waves reaching the eye from the object. The feelings in the

actual occasions in the retina are transmitted from occasion to occasion up the optic nerve to the percipient actual occasion in the brain. This actual occasion therefore prehends the preceding bodily occasions in the optic nerve—a constituent of which was the pattern or nexus of feelings originally constituted as the nexus of light waves passing from the fruit to the retina. Thus the fruit is perceived (prehended) by the brain occasion.

(This account omits all mention of Whitehead's notion of the two modes of perception—the mode of causal efficacy and the mode of presentational immediacy—and of symbolic reference. This is set out in *Process and Reality*, but more satisfactorily in *Symbolism: Its Meaning and Effect* (1928)).

So far, little beyond the "responsive phase" has been exhibited by this brain occasion. But now, in a high-grade conscious occasion there would be further activity of its mental pole. In the first instance, the eternal object correlated with the physical feelings of the fruit objectified in the percipient occasion will be a patch of color of a certain shape (a *sensum*). There will then be a secondary derivation of conceptual feelings from the primary one—such as the ideas of ripeness, edibility, etc. The subjective form of these conceptual feelings has the character of a valuation of the eternal objects—i.e. their value for the realization of the subjective aim of the actual occasion. (The *sensum*, and the characterization of the subjective form of the conceptual feelings, involve the distinction between the objective and subjective species of eternal objects. *P.R.*, 412.)

"The intermediate phase of self formation" (between the initial phase of reception of the past and the final stage of anticipation of the future) "is a ferment of qualitative valuation" (*A.I.*, 269). It



constitutes the supplemental phase mentioned earlier.

These feelings are successively unified by concrescence into the satisfaction of the subjective aim—which in this case is concerned with maintaining the well-being of the organism. This satisfaction (or rather, certain of its component feelings) is objectified into the actual occasions constituting the motor centers of the brain, resulting in the seizing and eating of the fruit. (This example of perception is the present writer's.)

#### *Originality of response*

In the case we have just described the feelings prehended by the percipient occasion in the brain included a mass of feelings such as those appearing physically as the metabolic processes in the optic nerve, etc. as well as those more particularly inherited from the nexus of light waves leaving the fruit. But the high grade living occasion which we are now considering can analyse this mass of data and concentrate, so to speak, on a particular constituent of it—namely, the visual sensum in its relation to its surrounding world. Hence the living organism can respond to individual components of a complex objective datum in a way in which an electron cannot.

Originality of response involves this bringing into definiteness of feelings which were vague in the initial phase of the concrescence. "By the originative power of the supplemental phase, what was vague, ill defined, and hardly relevant in causal efficacy, becomes distinct, well defined, and importantly relevant in presentational immediacy" (*P.R.*, 242). By bringing into prominence (paying attention to) physical and conceptual feelings, a richer influx of conceptual feelings ensues, from which a selective concrescence takes place, the selection being the selection of the

eternal objects which are relevant to the concrescence which is to satisfy the subjective aim (*P.R.*, 214). "A single occasion is alive when the subjective aim which determines its process of concrescence has introduced a novelty of definiteness not to be found in the inherited data of its primary phase" (*P.R.*, 145).

It will be noted that originality of response is limited in two ways. Firstly, the total kinds of eternal objects are given for the universe, and therefore the *possible* conceptual feelings are limited in this way. "There are no novel eternal objects" (*P.R.*, 30). (This does not mean, of course, that all possible modes of feeling have yet been realized in the world.) Secondly, conceptual feelings are derived from, relevant to, the physical feelings, either immediately, or mediately through other conceptual feelings. Ideas cannot gain ingress to the mind absolutely out of the blue. They must be suggested by feelings or ideas already present.

The notion of *relevance* is thus seen to be fundamental for Whitehead's conception of the appearance of novelty, but to attempt to expound it would be beyond the scope of this brief account. It is set out in Chapter III of *Process and Reality*. Briefly, however, relevance—in other words a mutual order among eternal objects—has to be accepted as the given condition under which creativity is able to produce an ordered world with evolutionary advance into novelty.

This selection of eternal objects takes place (at least potentially) in all actual entities. It is part of the way in which the subjective aim (final cause) expresses itself. But in non-living entities, the component conceptual feelings from which a selection can be made are so few and obvious that there is virtually no freedom of selection, and therefore simple re-enactment of the concrescence of the preceding

actual entity takes place, as described above.

#### NEXUS

Leaving now the life history of an actual entity, we must consider the conception of *nexus* a little more closely. A nexus is defined by Whitehead as "a set of actual entities in the unity of the relatedness constituted by their prehensions of each other" (Category of Explanation, XIV, *P.R.*, 32).

The simplest type of nexus is constituted by a single "route" or "strand"—that is to say, temporal succession—of actual entities—e.g.  $A_1-A_4$  in the diagram. Now take any particular entity,  $A_4$ .  $A_4$  prehends  $A_3$ . But  $A_3$  prehended  $A_2$ , therefore in prehending  $A_3$ ,  $A_4$  also prehends  $A_2$ 's prehension of  $A_1$ . This process can be continued back indefinitely. So it comes to pass that in prehending  $A_3$ ,  $A_4$  is prehending the whole of the preceding actual entities of the strand, as a unity. Any enduring object is thus necessarily a nexus.

Now consider a nexus containing two such strands,  $A$  and  $B$ , using the letters, without subscripts, to apply to the strands composed by  $A_1, A_2, A_3$ , etc. It might be helpful to exemplify these strands as chemical atoms (remembering that actually an atom consists of many strands—e.g. electrons and protons). When  $A$  and  $B$  are brought into the proper relations (concerning emphasis of mutual prehension) they unite into the nexus known as a molecule. In other words, the conceptual feeling derivate from the prehension of  $A$  and  $B$  in one datum is the feeling of the eternal object, molecule of  $AB$ . Now we will suppose that  $A_5$  and  $B_5$  come into that relation. These are succeeded by  $A_6$  and  $B_6$ .  $A_6$  prehends  $A_5$  and  $B_5$  as initial data which undergo concrescence into this single objective

datum. The prehension by  $B_6$  of  $B_5$  and  $A_5$  is of a corresponding nature.

It follows that every nexus is accomplished for the first time during the concrescence of an actual entity (*P.R.*, 325). It is a concrescence of separate feelings into a unity. But once accomplished, it can in future be objectified as a unity in other actual entities. The act of combination of the two atoms into the molecule is the original formation of the nexus. But in future the nexus can be objectified as such, the objectification appearing physically as the properties of the molecule.

It is in this conception of the unity of a nexus that we strike the main idea of theories of organism as usually understood by biologists, namely, the idea that the whole is more than the sum of its parts, and indeed imposes its own character on its parts. As Ritter puts it, the whole acts causally on its parts, as well as being acted on causally by its parts.

This is only understandable if we get away from the idea of substance and fix our attention on process. We must not think of the molecule as composed of ultimate particles of matter in motion. But the molecule is a pattern of processes, and each constituent process conforms to its place in the pattern, and resists factors tending to alter it. This conformity is, in Whitehead's terminology, conformity of the subjective aim and form of each actual entity to the pattern of feelings provided for it by other members of the nexus (as prehended from its own perspective). Its resistance to alteration of the nexus is the objectification of its own feelings as determinant agents in the other actual entities of the nexus. As Whitehead says in a much quoted passage (*S.M.W.*, 116), "An electron within a living body is different from an electron outside it, by reason of the plan of the body."

Indeed, from one point of view White-

head's philosophy may be characterised as showing how things (*nexūs*) have subjective multiplicity and objective unity. The number of actual entities composing the complex nexus known as a dog is colossal. Yet the rabbit perceives the dog, not as a collection of separate entities, but as a dog. And it must be remembered that this perception, or prehension, of the nexus as a unity is not confined to external actual entities. But the actual entities composing the nexus itselfprehend the other entities in the nexus not as individuals, but as a unity, in which of course the component parts have not necessarily lost their identity.

Whitehead's thesis that all actual entitiesprehend all other actual entities either directly, or through the mediation of other actual entities means that the whole Universe is a nexus. "If we allow for degrees of relevance, and for negligible relevance, we must say that every actual entity is present in every other actual entity" (*P.R.*, 69). But there appears to be nothing in his basic conception of the nature of actual entities which necessitates the formation of subordinate *nexūs* within the universal nexus. Whitehead calls his philosophy a Philosophy of Organism. There appears, however, to be nothing in the nature of reality as he conceives it which necessarily leads to the formation of organisms in the plural—i.e. of the things we are acquainted with. It is a peculiarity of the extensive continuum of our own universe and epoch that leads to certain types of actual entities having certain special relations to each other, and so producing electrons, molecules, rocks and men. A universe of actual entities of the same metaphysical nature as our own seems to be conceivable in which no *nexūs* within the universal nexus were formed. Such a universe would presumably possess

a uniform and unchanging texture throughout.

### *Societies*

Whitehead recognizes several types of *nexūs*. In one sense, as we have seen, the whole universe is a nexus. But there are others of a more intimate type. Such are called "societies". In a society the internal relations are so close that it is relatively independent of the rest of the world—that is to say, of its environment. It is worth while quoting Whitehead's description of a society, and certain other *nexūs*.

A nexus enjoys "social order" where (i) there is a common element of form illustrated in the definiteness of each of its included actual entities, and (ii) this common element of form arises in each member of the nexus by reason of the conditions imposed upon it by its prehensions of some other members of the nexus, and (iii) these prehensions impose that condition of reproduction by reason of their inclusion of positive feelings of that common form. Such a nexus is called a "society," and the common form is the "defining characteristic" of the society. . . . The common element of form is simply a complex eternal object exemplified in each member of the nexus (*P.R.*, 46).

A nexus enjoys "personal order" when ( $\alpha$ ) it is a "society," and ( $\beta$ ) when the genetic relatedness of its members orders these members "serially". . . . Such a nexus is called an 'enduring object' (*P.R.*, 47).

For example, the strands *A*, *B*, *C* in the diagram each have personal order.

It would appear that any society which endures (i.e. lasts beyond the life history of a single set of contemporary entities) must have a certain degree of personal order.

"An ordinary physical object, which has temporal endurance, is a society. In the ideally simple case, it has personal order and is an 'enduring object'. A society may (or may not) be analysable into many strands of 'enduring objects'. This will be the case for most ordinary physical objects" (*P.R.*, 47). Such *nexūs*, analys-

able into strands, are "corpuscular societies" (*P.R.*, 48).

A structured society (*P.R.*, 137) is a society containing (1) subordinate societies, and (2) subordinate nexūs of a lower type than societies. Such a structured society is illustrated by a living cell, in which

(1) the subordinate societies are nexūs which could have retained their dominant features in the general environment which is the universal nexus, apart from the special environment of the structured society of which they form a part.

(2) the subordinate nexūs are nexūs which present no features capable of sustaining themselves apart from the special environment provided by that structured society.

Subordinate societies are the inorganic nexūs within the living cell—for instance, a molecule. Subordinate nexūs are "entirely living" (*P.R.*, 143). Thus life does not pertain to the cell as a whole, but to subordinate nexūs within it.

Physical Physiology, according to Whitehead, deals with subordinate societies—i.e. the subservient inorganic apparatus.

Psychological Physiology seeks to deal with the "entirely living" nexūs, partly in abstraction from the inorganic apparatus, partly in respect to their response to the inorganic apparatus, and partly in regard to their responses to each other (*P.R.*, 144).

#### LIFE

Whitehead's conception of *life* may conveniently be considered here. A living organism is always a nexus of the grade of a society, containing both subordinate societies and subordinate nexūs, as we have just seen. Life is characteristic of one or more of these subordinate nexūs.

In the case of the higher organisms—for instance, the vertebrates—one of these subordinate nexūs has a peculiarly dominant function. The mind of man, for instance, is such a dominant subordinate nexus. It has personal order, for it is an enduring object, exhibiting memory and personal identity. The stream of actual occasions of which it is composed are called *presiding occasions*. Thus he says (*P. R.*, 152).

In a living body of a high type there are grades of occasions so co-ordinated by their paths of inheritance through the body, that a peculiar richness of inheritance is enjoyed by various occasions in some parts of the body. Finally, the brain is co-ordinated so that a peculiar richness of inheritance is enjoyed now by this and now by that part; and thus there is produced the presiding personality [referred to below as the presiding occasion] at that moment in the body. Owing to the delicate organization of the body, there is a returned influence, an inheritance of character derived from the presiding occasion and modifying the subsequent occasions through the rest of the body.

The endurance of mind is achieved in the same way as that of any other "enduring object"—namely by inheritance from one actual entity (presiding occasion) to another.

Whitehead locates the living occasions in the "empty spaces" of cells (*P.R.*, 138) or even "wandering in 'empty space' amid the interstices of the brain" (*P.R.*, 481). It would appear that his reason for this disconcerting suggestion is consideration of the originality of response characteristic of living occasions. It appears that by empty space he does not mean space unoccupied by actual entities, but unoccupied by any corpuscular society. An actual entity arising in contiguity with such a society is overwhelmingly constrained into conformity with its objectifications. But arising in space which is not so occupied, it will not be thus dominated and so will have greater freedom

of action. This at any rate is what the writer conceives to be the meaning of *P.R.*, 147.

The lower forms of animal life, and all vegetable life, according to Whitehead show no evidence of the dominance of any included personal society (*A.I.*, 264)—i.e. of an enduring stream of presiding occasions. Rather, their life has the form of a democracy of living subordinate nexūs (together, of course, with subordinate societies providing the subservient inorganic apparatus), which, unlike the case of the higher animals, are not dominated by presiding occasions.

As regards the character of the actual entities themselves which may be called living, or components of a living society, we note first that in *Process and Reality* life is ascribed to single actual entities, while in *Adventures of Ideas* it is ascribed to groups of coördinated actual entities.

A single occasion is alive when the subjective aim which determines its process of concrescence has introduced a novelty of definiteness not to be found in the inherited data of its primary phase (*P.R.*, 145).

Those activities in the self-formation of actual occasions which, if coördinated, yield living societies are the intermediate mental functionings transforming the initial phase of reception into the final phase of anticipation [in *P.R.* called satisfaction—see *A.I.*, 248]. In so far as the mental spontaneities of occasion do not thwart each other, but are directed to a common objective amid varying circumstances, there is life. . . . It is evident that according to this definition no single occasion can be called living (*A.I.*, 266).

The actual entity itself, whether we call each one living, or only a component of a living group of entities, is characterised by enhanced activity of the mental pole, whereby there is a richer development of conceptual feelings of eternal objects, some of which may be novel in the sense that they are not in the original objective datum. From these eternal objects a selection is made of those ap-

propriate to the fulfilment of its subjective aim. In all actual entities there is, as we have seen, a mental pole, and conceptual feeling of eternal objects, with potential power of selection (positive or negative prehension)—but this is of negligible force (at any rate in the average of the huge numbers of actual entities composing even the smallest of observable inorganic bodies or events), and therefore simple re-enaction of the process of the preceding actual entity which is dominant in the initial data takes place. Endurance of inorganic objects is brought about thus, but continues only so long as the initial data are repeated at least in their dominant features for each successive generation of actual entities. Should this change, the changed prehensions of the succeeding actual entity will result in a corresponding change in the concrescence—and the molecule, for instance, is decomposed.

Living organisms, however, can achieve endurance, not merely by re-enactment, but in face of changed environment (initial data) by virtue of this greater power of conceptual feelings for eternal objects not to be found in the initial data, with selection among them. Thus living organisms adapt themselves to their environment by originative action.

It is important to realize that Whitehead does not consider that a nexus of actual entities can itself be considered as an actual entity of a higher order with a subjective aim of its own.

Commenting on this, Emmet remarks (p. 184):

Are not all these descriptions of the kinds of prehensions involved in a concrescence applicable rather to the nexus of actual entities as a whole, taken over a long spell of its history? We can with some plausibility talk of an animal as having a subjective aim; but can we seriously use the same language of an "electronic occasion"?

*Presiding occasions*

As we have seen, in one sense a higher animal can be said to have a subjective aim transcending the subjective aims of all its component actual entities, for its behavior is governed by a "presiding occasion"—or if the mind is not merely a momentary flash, a route of presiding occasions with "inheritance from presiding occasion to presiding occasion." This seems at first sight reminiscent of the vitalistic view of the body as a machine controlled by the mind as mechanic, and Whitehead's theory as applied to the behavior of the higher organisms seems to become less a theory of organism in the usual sense of the term, than a theory of the manner in which information is conveyed from the body to the mind, and instructions conveyed back again from the mind to the body. But there is actually this fundamental difference from the older point of view, that the body-mind relation involved is not an *ad hoc* hypothesis, but an illustration of the nature of actual entities and of the relation between them which is universal throughout nature.

As we have seen, however, this conception of presiding occasions is not essential to Whitehead's conception of the unity or wholeness of an organism, whether living or not living. It is indeed only the limiting case, for this wholeness is always brought about by the prehensions and objectifications of the component actual entities, certain classes of which may be more important in this regard than others. The special dominance of the presiding occasions constituting the mind of a higher animal can be connected by grades with the case of a simple chemical molecule where the task is presumably more equally shared by all the component actual entities. The case of the life (apart from conscious mental life) of a multicellular

organism occupies an intermediate position, for he considers that there is no life of the organism as a whole above that of its individual cells. Within each cell certain subordinate nexūs are dominant in preserving the cell as a living organism. The organism as a whole is presumably to be conceived as compounded out of its living cells on the same principle as any other nexus. Each cell (through the agency of the actual entities in its living subordinate nexūs) lives its own life in conformity with its environment (by its prehensions of the rest of the nexūs) and has its own "end-in-view," which is essentially to provide by its objectifications an environment for the other cells of the organism such that they in turn, while living *their* own lives will at the same time continue to provide an environment suitable for the continuance of the life of the cell in question.

## SUMMARY

The features in Whitehead's system which will probably appear of most immediate significance to theoretical biology may now be enumerated.

1. Reality consists in experience or feeling, rather than in substance supporting qualities. This has fundamental consequences for the problem of the body-mind relation, which has always stood like a lion in the path of the biologist who is trying to form a conception of the living organism.

2. The process of experience is atomic, and yet of a nature to lead to a universal relatedness between the atoms of process (actual entities) under the guise of the objectification of preceding in succeeding actual entities. This is efficient causation.

3. Final causation (subjective aim) operates within each actual entity. Herein

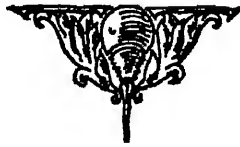
lies the teleology of the universe (cf. *A.I.*, 249).

4. Since the subjective aim of an actual entity is not merely at self-completion, but at self-realization as an agent determinant of other actual entities, it follows that efficient causation is referable to the final causation of an agent.

5. Organisms, whether living or not, are *nexūs*. The general notion of *nexūs* is implied in the notions of prehension and concrescence—that is to say, in the nature of an actual entity itself. An account

of the various types of *nexūs* actually found in nature is given above.

6. The difference between living and non-living organisms is one of degree only. All actual entities have a measure of autonomy in their self-realization out of their data, but this factor is of negligible importance in the case of non-living entities owing to the simplicity of the subjective aim and objective datum, which give little scope for selection among the conceptual feelings of the relevant eternal objects.





## THE FUNCTIONS OF THE PYRAMIDAL TRACTS

By CLYDE MARSHALL

*Department of Anatomy, Section of Neuro-Anatomy, Yale University School of Medicine*

IN SPITE of the fact that the term "pyramidal tract" is commonly used in neurology, a certain confusion seems to exist as to its proper definition. Thus some define it as all those fibers passing downwards through the pyramids of the medulla to the spinal cord, or as the sum total of all cortico-spinal fibers. Others define it as consisting of only those cortico-spinal fibers arising from a certain region in the cerebral cortex, such as the primary motor cortex or area 4 of Brodmann. By the last definition any cortico-spinal fibers passing from the premotor area (area 6 of Brodmann) or from the postcentral gyrus would be regarded as "extra-pyramidal."

On historical grounds the priority goes to the first definition, for the name arose not as many suppose, because the tract arises from pyramidal cells in the cerebral cortex, but because it represents a continuation of the pyramids of the medulla. The name was given, indeed, before any connection of the tract with the cerebral cortex was established. Türck (1851, 1853) who first described it, gave the name "pyramidal-lateral-column-tract" for what is now known as the crossed pyramidal tract, and the name "capsular-anterior-column-tract," to what is now called the direct pyramidal tract or the tract of Türck. He regarded these two as descending tracts which arose in the region of the basal ganglia, particularly in the lenticular nucleus. Flechsig in 1876 described both components under the name "pyramidal tract." He agreed with Türck as to its probable lenticular origin,

but since he could not be certain of possible cortical connections he declined to use the term "lenticular-nucleus-lateral-column-tract" which he otherwise preferred. It was not till a later date (1877, 1881) that Flechsig brilliantly demonstrated by the myelogenetic method the connections of the pyramidal system with the cerebral cortex, particularly the precentral gyrus and the paracentral lobule.

The experimental anatomists following Flechsig agree in defining the pyramidal system as those fibers passing through the pyramids into the spinal cord or as the sum total of the corticospinal system. Agreement has not been reached, however, as to the extent of its origin from the cerebral cortex. Campbell ('05) on the basis of his studies on amyotrophic lateral sclerosis (which were later proved to be incorrect) and some other evidence, affirmed that the tract arose exclusively from the giant cells of Betz within the cytoarchitecturally defined motor area.

The term "motor area" or "motor cortex" is an unsatisfactory one, since four definitions have been given it as follows: (1) A specific cytoarchitectural cortical area, such as area 4 of Brodmann, or area FA of Economo; (2) the area of origin of the pyramidal tract; (3) the electrically excitable area of the cortex; (4) that cortical area which when removed will give the maximal paralysis. In the present discussion the first definition is consistently used.

Holmes and May ('09) from their studies of chromatolytic cell changes following spinal cord lesions in a large variety of ex-



perimental animals and in human cases, reached the same conclusions as Campbell. The majority of investigators, on the other hand, have described pyramidal fibers arising from a larger cortical region than the cytoarchitecturally determined motor area or Brodmann's area 4. Thus Flechsig's ('05, '20) myelogenetic area from which the pyramidal tract is stated to arise passes forward on to the premotor area or Brodmann's area 6; and O. Vogt ('06) describes a few pyramidal fibers arising from the post central gyrus. Dejerine ('01), Monakow ('05, '14) and Minkowski ('23-'24) describe pyramidal fibers descending from both the premotor and post-rolandic areas following cerebral cortex lesions. Schröder ('14) found, in contrast to Holmes and May, that spinal cord lesions produced retrograde changes in other than the Betz cells and that they extended into the pre-motor region. Economo and Koskinas ('25) conclude from various lines of evidence that the Betz cells are not the sole cells of origin of the pyramidal tract and that the area of origin is probably larger than cytoarchitectural motor area.

If we thus differentiate between the definition of the pyramidal tract and the conclusions reached regarding its origin, it readily becomes apparent that throughout the experimental literature the pyramidal tract is *defined* according to the first definition with which the discussion began. Any definition which would exclude cortico-spinal fibers, from say, the premotor area (area 6 of Brodmann), as "extrapyramidal," has no historical sanction and can be defended only on a purely arbitrary basis. In addition, the *conclusion*, that the tract in question arises solely from the cytoarchitecturally defined motor area rests on a very insecure foundation.

#### EXPERIMENTAL LESIONS OF THE PYRAMIDAL TRACTS

Experimental lesions of the pyramidal tracts free from associated damage to other descending motor systems can be made only by attacking them in the pyramids of the medulla. Lesions of the cytoarchitecturally defined motor cortex are unsatisfactory for this purpose for several reasons. The unavoidable associated injury to the sensory and associational systems is obvious. In addition there descend from the motor area many other cortico-fugal fibers besides the pyramidal as Mellus ('95) long ago pointed out. This author stated that of the descending degeneration resulting from the removal of the thumb area in the monkey, as much as half or more stopped at the substantia nigra. There is also a significant motor area-rubral system as Rothmann ('01) and Marshall ('34 b) have shown. These fibers must of necessity be damaged with the pyramidal in motor area lesions. Finally, for reasons pointed out above, it has not been satisfactorily demonstrated that the removal of the motor area will cause a degeneration of the pyramidal system in its entirety.

Although the number of experimenters who have made lesions in the motor cortex is large, those who have attempted to interrupt the pyramidal tract in the medulla are relatively few. The first to produce experimental lesions in the pyramids—although he had no knowledge of the existence of the definitive pyramidal tracts—was Magendie (1838). He described the findings as follows:

I divided directly one of the pyramidalia in two living animals, reaching it through the fourth ventricle. I could not remark any sensible lesion in the movements, particularly no paralysis ensued, either on the wounded or opposite side. I did more, I divided entirely and across, the two pyramidalia about the

middle of their length, and no apparent derangement in the motions followed. I observed only a little difficulty in walking forwards.

Some years later Schiff (1858) criticized Magendie's work on the grounds that cutting through the midline of the medulla from the fourth ventricle destroyed many other important structures besides the pyramids. He devised two operative approaches and cut, in rabbits, the pyramids, or the pyramidal decussation without splitting the medulla. He stated that as a result of his operations it has been shown "that neither a transitory nor a permanent noticeable paralysis necessarily follows, and that we are not entitled to endow the pyramid with the physiological properties of the anterolateral column, insofar as they are known at present." No anatomical evidence was offered by either Schiff or Magendie to show the extent of their lesions.

Of more recent date three different operative procedures have been used. These are (1) cutting the pyramids above the decussation from a ventral approach, either through a longitudinal incision in the neck (Starlinger, '95) or by the transphenoidal route (Ranson, '32); (2) cutting the pyramidal decussation through a ventral neck approach (Rothmann, '00); (3) cutting the pyramidal decussation by splitting the medulla sagittally in the midline from its dorsal surface (Magendie's operation). The first operation is obviously the method of choice, since the second and third must leave uncut the uncrossed pyramidal fibers in the lateral column of the cord. These fibers, now often forgotten, were long ago demonstrated in the dog by Muratoff ('93); in the monkey by Sherrington ('94), and in the cat by Boyce ('95). The third operation must in addition cut many other fibers. Even the first procedure, to be

crucial, should be bilateral, for only by this method is it possible to remove completely all pyramidal innervation from even one side of the body.

#### PYRAMIDAL LESIONS IN THE DOG

The first anatomically controlled experiment on dogs, and indeed on any animal, was made by Starlinger ('95, '97). He cut both pyramids above the decussation in six animals and found initially a certain number of symptoms which gradually declined, leaving the animal in about two weeks essentially normal. Soon after the operation many of the animals could run and jump, although some are reported as being slower, more cautious, and more deliberate than normal. One is reported as jumping down heavily, another as showing marked postural defects such as crossing the forelegs, and a third as having rolling movements for a few days. Any motor weakness present was in general very slight, and spasticity did not appear. The symptomatology is reported as being less severe and of shorter duration than that following removal of the motor areas. Eventually there were found no symptoms which could be attributed to the absence of the pyramids. Histologically there was a degeneration of the pyramidal tracts more or less complete and traceable varying distances down the cord. In some cases there was damage to the medial lemniscus, the interolivary region and the median raphé.

Rothmann ('00, '01, '07) sectioned the pyramidal decussation from the ventral approach in a number of dogs. He found that a slight weakness and "ataxia" was initially present which, however, was practically over in two or three weeks. The "Berührungsreflexe" of Munk, reflexes of flexion and elevation of the

limbs incited by stroking the hairs on the dorsum of the feet, were initially absent, but returned as a rule in four or five days.

Schüller ('06) made unilateral lesions in the pyramids in two dogs. There were relatively few symptoms. A tendency to inward rotation of the hip and shoulder was present, and when the animal was moved to one side or the other ("Flankengang") there was a slowness of movement in the affected limb, particularly in adduction. There was no spasticity. The "Berührungsreflexe" are reported as being more active on the affected side.

Finally Bechterew ('09) in his *Funktionen der Nervencentra*, states that Protopopov has cut the pyramids on both sides with a gradual return of even isolated movements. The operative method is not given, nor is any histological proof of section provided.

#### PYRAMIDAL LESIONS IN THE CAT

The earliest reports of pyramidal lesions in the cat were made by Redlich ('97) and Probst ('01). Neither gives any anatomical or physiological details of his findings. Redlich says only that he has confirmed Starlinger's observations in the cat, and Probst states merely that destruction of the pyramidal tracts in the medulla brings about no fundamental disorders of motility. Of more recent date experiments on cats have been made by Langworthy ('28); Pike, Elsberg, McCulloch and Rizzolo ('29); Pike, Elsberg, McCulloch and Chappell ('30); Ranson ('32); and Marshall ('33, '34).

Langworthy ('28) cut the pyramidal decussation by a sagittal splitting of the medulla approached from the dorsal surface in nine cats. The results were severe, more so than in any of the cases previously reported. The foot pads were often turned under at the foot and ankle. No extensor tonus was present. The animals

steadily improved with time. In general, they showed greater defects than those with the motor areas removed, a finding directly opposed to that of Starlinger, Rothmann and Redlich, and probably dependent upon the different operative procedure used. Histologically there were found injuries to the pyramidal tracts, the medial lemniscus and the olivary fibers.

Pike, Elsberg, McCulloch and Rizzolo ('29), and Pike, Elsberg, McCulloch and Chappell ('30) used the same operative approach as Langworthy. They found that "the immediate effects of splitting the decussation of the pyramids are manifested in a severe motor disability differing somewhat from that seen after bilateral ablation of the cortical motor areas. After motor area removal there is always extreme flaccidity of the muscles, while after this operation there may be occasional spasticity of the forelimbs." The rate of recovery is not clear from their reports. In one instance, it is said that "after 10 to 14 days the animal begins to walk about" and in another, "from 10 to 14 days after operation the animal again walks about fairly well." Eventually there was less disorder than that occurring from removal of the motor areas. Histologically, the pyramidal tracts were found degenerated.

Ranson ('32) cut one pyramid by the transphenoidal route in eleven cats. The animals were allowed to live only one day and hence no recovery phenomena are available. Shortly after the operation "all but one were able to walk and most of them walked very well." None showed signs of hypertonus in walking but when suspended in a sling, a certain degree of rigidity was apparent, which was greater in the fore than in the hind limb. This finding of increased extensor tone is in agreement with an

observation of Ranson, Muir and Zeiss ('32) who found, in one animal, that a lesion in the spinal cord which partly severed the cortico-spinal tract and did not damage the rubro-spinal fibers produced a definite spasticity in the affected limbs.

Marshall ('33, '34) made twelve bilateral and five unilateral lesions in the pyramids after the method of Starlinger. Severe disorders of motility were absent except in a few animals, and in these they were confined to the first two days. There were, however, a number of initial defects, which gradually disappeared, partly or entirely, during the two or three weeks the animals were allowed to live. The initial defects included the following. There was an occasional transient staggering and a spontaneous placing of the feet in abnormal positions. Abnormal postures imposed upon the animal were not promptly corrected. There was a tendency towards a slight stiffness in the gait and under certain conditions, e.g., when suspended in a sling, a definite increased resistance to passive flexion (extensor tonus) was present. There was a peculiar slowness in motion, and the general activity of the flexor muscles was reduced. The "Berührungsreflexe" of Munk and the placing and hopping reaction of Rademaker were also defective. The defects, on the whole, were less severe than those following removal of the motor cortex. Histological studies showed degeneration of the pyramidal tracts and a varying amount of injury to the medial lemniscus and interolivary fibers.

#### PYRAMIDAL LESIONS IN THE MONKEY

Lesions have been made in the pyramidal tracts in monkeys by Rothmann, Schüller, and Schäfer. Rothmann ('01-'07) cut the decussation by the dorsal

approach of Magendie, finding the ventral operation too difficult in these animals. He observed an initial defect, but a return of even the finest finger adjustments after eight to fourteen days. He made many combined operations, cutting the decussation along with other parts of the central nervous system and came to the final conclusion that the pyramidal tracts in the monkey possess no specific functions which cannot be taken over in large measure by the extrapyramidal pathways. Only in the speed of its movement is the monkey without pyramidal tracts behind its normal fellow, "a fact which, in view of the marked reduction in the total area of the motor pathways from the cerebral cortex to the spinal cord is not surprising." Rothmann ('04) attempted to cut the pyramids in chimpanzees but without success.

Schüller ('06) succeeded in making unilateral lesions in one pyramid from the ventral approach in two monkeys, one complete, the other incomplete. The defects were more severe here than in his dogs and more so than in Rothmann's monkeys. After two weeks prehension of food was carried out poorly by the affected hand, the legs were used stiffly and awkwardly in movement, and there was the same difficulty in sideward motion ("Flankengang") seen in the dogs. This test by Schüller appears to be the forerunner of Rademaker's hopping reaction (Hinkebein).

Schäfer in 1900, in a footnote in his *Textbook of Physiology* states briefly that he was unable to confirm Starlinger's findings in the monkey. In 1910, he described in detail the effect of injury to the pyramids in three of these animals. In two, the damage was chiefly unilateral, and in one, both pyramids were almost completely severed. He was particularly interested in "voluntary" movement and

for this he employed three tests. First, the ability to pick up currants from the floor and to carry them to the mouth; second, the tendency of the limbs to reach for contact on swinging or dropping the animal towards a cage or to the floor; and third, the use of the hands in grasping. He considered the second the best test for voluntary movement in the hind limb, the third as variable and rather dependent upon the disposition of the animal. Schäfer states, "It is noteworthy that after 21 days there is manifested a considerable amount of voluntary movement of the paralyzed arm, but none up to 28 days of the corresponding leg, unless its increased facility in walking, climbing and leaping is to be taken as evidence of such recovery."

#### THE PATHWAYS MEDIATING THE RESPONSE ON ELECTRICAL STIMULATION OF THE MOTOR CORTEX

The experiments reported above relate entirely to the functional defects produced by lesions of the pyramidal system in the medulla. This does not, however, cover all the functions assigned to the pyramidal tracts for they have long been regarded as mediating the response on electrical stimulation of the motor cortex. Indeed they are often regarded as being the only tract capable of underlying this reaction, although the bulk of experimental evidence is against this conclusion as will be seen from the sections to follow. These experiments are mostly of an acute nature and were performed on rabbits, cats, dogs, and monkeys. As in the previous sections, the findings in the different animals will be reported separately.

#### EXPERIMENTS ON RABBITS

The central nervous system pathways mediating the response on electrical stim-

ulation of the motor cortex of the rabbit became a subject of experimental investigation shortly after the publication of Fritsch and Hitzig's monograph in 1870. Gliky ('76), working in the laboratory of Eckhard in Giessen, made sagittal sections in the midline of the cerebrum, which extended as far backwards as the posterior colliculi. He found the usual contralateral responses to persist after this lesion and concluded that the decussation of the pathways underlying the reaction must lie caudal to the posterior limit of his sections.

Balighian ('79), also working with Eckhard, traced the pathways further. He made hemisections at various levels of the medulla oblongata from the calamus scriptorius to the tuberculum acousticum. In some, he added to a transverse lesion in the tuberculum acousticum a sagittal midline section which passed from this level caudally to the calamus (fig. 1). When these lesions were made on the right, thus sectioning the right pyramidal tract—meaning the pyramidal tract arising in the right cerebral cortex—he found that stimulation of the right motor cortex gave a large response on the left side, while stimulation of the left cortex gave only a feeble movement on the right. He concluded that the crossing of the fibers mediating the reaction must be spread out over a long distance, which extended from above the tuberculum, acousticum to below the calamus scriptorius. Most of the crossing must take place above the medulla and probably, he says, in the pons. Its lower border he did not determine but concluded that there was no evidence that it was "lower than the atlas." A reference to the figure will show that the results could be explained on the basis of the preservation of either the pyramidal or the cortico-rubro-spinal system. The

findings would further suggest that the cortico-rubro-spinal tract must be the more important since a greater response was obtained on the side on which it was intact.

By far the most prolific writer of this early period was Brown-Séquard (1879-1889) who vigorously opposed the two theories then current as to the pathways involved. These were first the doctrine of Ferrier, that the essential pathway was the pyramidal tract with its decussation in the medulla, and second that of Schiff, and Lussana and Lemoigne, who argued that it was not the pyramidal tract but another with its decussation in the pons. Brown-Séquard made hemisections of the medulla, pons and cerebral peduncles and claimed that not only were contralateral movements still possible from stimulation of the motor area on the side of the lesion, but that the responses were even greater than before. The response was unaffected by section of the corpus callosum. On the other hand, the middle third of this structure was electrically excitable and from this and other evidence he concluded that the corpus callosum carried an alternative pathway for movement. He made midline sagittal sections of the pons and even "from the superior part of the cerebral peduncles to below the pyramidal decussation" (Fig. 2a) and found—provided the animals survived—movements still possible from cortical stimulation, although much reduced.

In addition to these single lesions Brown-Séquard combined two or more sections and claimed some astounding results. Thus a combined midline section of the pons with a hemisection of the right half of the medulla (Fig. 2b) did not abolish the excitability of the right motor cortex. A combined section of the corpus callosum with a hemisection of the right half of the pons (Fig. 2c) did not abolish the

excitability of either cortex, although the response in the contralateral limb was smaller on stimulation of the right hemisphere as compared with that of the left. Even two hemisections of the brain stem on different sides, one high up in the pons on the right, the other in the middle of the medulla on the left (Fig. 2d) not only failed to suppress the cortical response but in some cases actually aug-

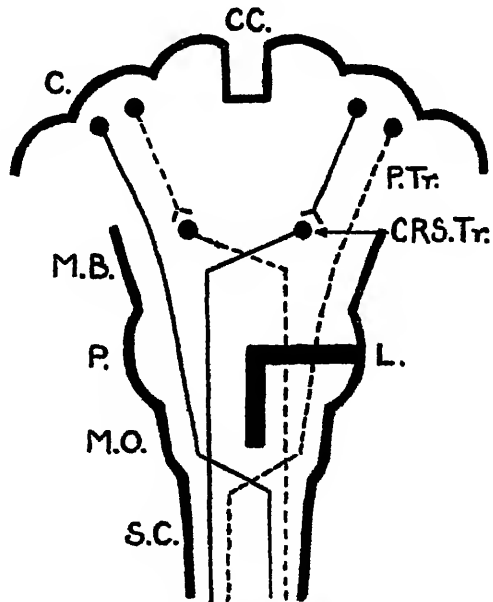


FIG. 1. BALIGHIAN'S EXPERIMENTS

C—cerebral cortex. CC—Corpus Callosum. CRS.Tr.—Cortico-rubro-spinal tract. L—lesion. M.B.—midbrain. M.O.—Medulla oblongata. P—Pons. P.Tr.—Pyramidal Tract. S.C.—Spinal Cord. Tracts in uninterrupted line are functional; those in interrupted lines have been sectioned and are non-functional.

mented it. A reference to figure 2 will show that of the four cases shown, two, (b) and (c), could be accounted for by the preservation of either the pyramidal or cortico-rubro-spinal systems. In (a) and (d) all of these tracts are cut, and the response must be mediated by other pathways.

In 1889 Brown-Séquard published his classical paper on section of the pyramids

in the medulla and of all of the medulla except the pyramids. He used rabbits and dogs, and found that after sections of the pyramids alone the response from cortical

on the basis of this and all his previous work that the pyramidal tracts were certainly not the only pathways mediating these reactions, that they were not even

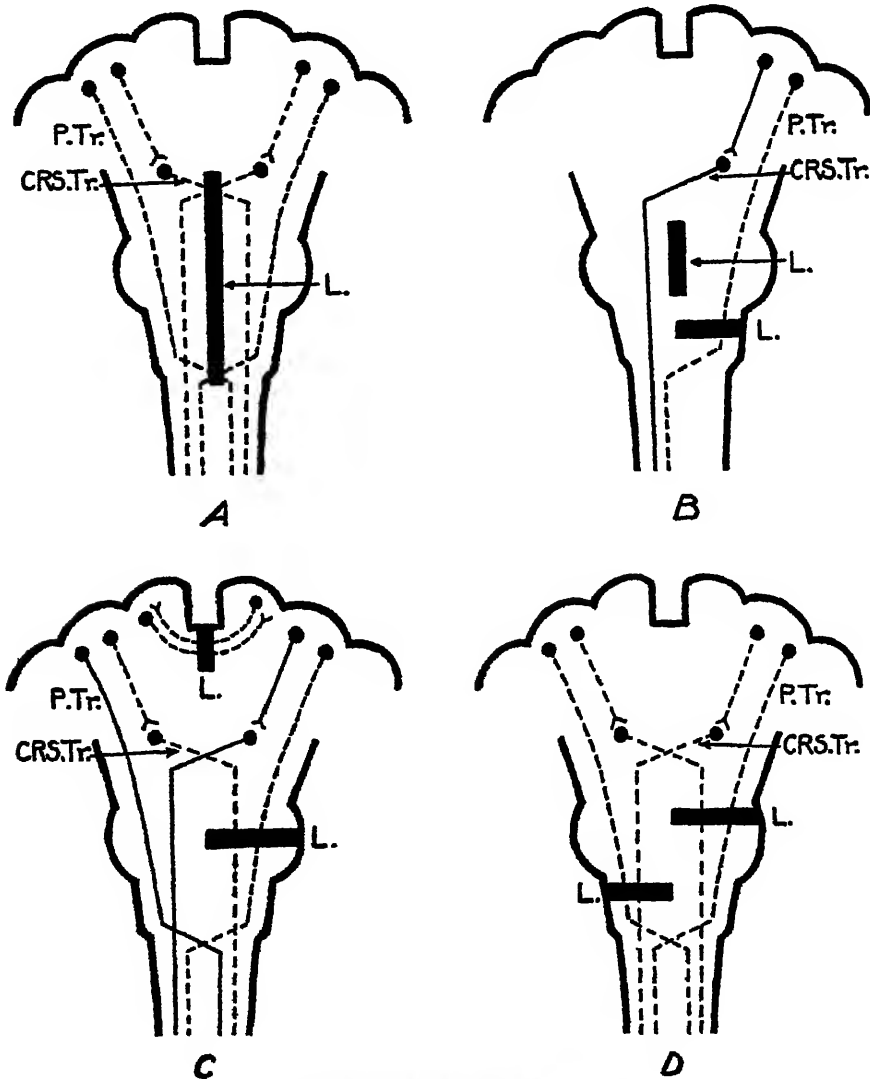


FIG. 2. BROWN-SÉQUARD'S EXPERIMENTS  
Explanation in text. Lettering as for Fig. 1

stimulation was as great or almost as great as before. After section of all but the pyramids a response was still present but considerably reduced. He concluded

the chief ones; and that the connections between the brain and spinal cord were more numerous than had been commonly supposed. He violently flayed the phys-

iologists and clinicians of his time who continued to uphold the doctrine of any single localized pathway for these reactions. In criticism it should be noted that he gives only meager accounts of his methodology. He appears not to have differentiated between discrete isolated movements and convulsive reactions, and he provides no objective evidence to show the extent of his lesions. Indeed, one does not know how this latter point was determined.

The observations so far reported refer to the movement in the contralateral limbs from stimulation of one motor area. But homolateral responses had also been observed which were thought by some to be due to the excitations of the opposite cerebral hemisphere by way of the corpus callosum. Exner ('81), however, demonstrated in rabbits, that the homolateral response was not altered by section of the corpus callosum, or even by complete removal of the opposite cerebral hemisphere. He concluded, therefore, that the innervation of the homolateral limb came directly from the cortex stimulated.

Steffahny ('88) continued the investigations started by Balighian. He determined the lower limit of the decussation of the fibers underlying the responses in the contralateral limbs and their position in the upper cervical cord. The lower limit was found to only a minimal amount (a few millimeters) below the tip of the calamus scriptorius and the pathway in its course below this decussation shifted its position. Just below the calamus it appeared to be almost entirely within the anterior column, while at the level of the 4th cervical segment it was confined to the lateral column. This description fits fairly closely the pyramidal tract although the author makes no reference to it. The pathway for homolateral movement passed along with that for the contralateral at

the levels studied. The careful description of method by this author forms a striking contrast to that of Brown-Séquard.

#### EXPERIMENTS ON DOGS

The experiments on rabbits were largely confined to the determination of the pathways for movement on the contralateral side of the body, although a few were aimed at the determination of these for homolateral movement. In the dog, a considerable number were devoted to this latter problem. For convenience in description they will be separated from the others and will be described later.

One of the first to investigate the pathways for contralateral movement in dogs was Brown-Séquard, and some of the experiments reported in the previous section were performed on these animals as well as on rabbits. The exact ones are in most cases a matter of doubt since the author is so scant on the details of his methods. The essential findings, however, must be assumed to be no different from those already reported, since the author makes no mention of any differences in his discussion of his results.

Schiff ('83), in addition to the experiments with chronic animals already reported, made a number of acute experiments on dogs. He reports an animal in which prior to a section of the lateral column of the cord the discharge of four Leclanché elements applied to the motor cortex produced a large movement in the contralateral side, while after the lesion a current of this strength had no effect. With increasing strengths, homolateral movements first appeared until finally when fourteen elements were used "a general reaction of pain" appeared in which the contralateral limbs weakly participated. These experiments of Schiff are the first to give evidence that interruption of the



tracts of the lateral column including both the pyramidal and rubro-spinal systems will render the contralateral cortex inexcitable for discrete movements.

Dupuy ('86) reported sectioning one "peduncle" in three dogs. Stimulation of the cortex on the side of the lesion with a coil at 12 cm. produced light movements on the contralateral side and when the coil was increased to 5 cm. a violent epileptiform convulsion occurred which involved the whole animal. The exact amount sectioned is not clear from the report.

Starlinger ('95, '97) stimulated on the seventeenth day the motor area of one of his animals in which both pyramids had been removed. He obtained a "prompt response" in the contralateral extremities and concluded, therefore, that this reaction was not mediated solely through the pyramidal tracts.

Stoddart ('97) sectioned the pyramidal decussation in twelve dogs and obtained movements in the contralateral hind legs, but none in the forelegs or trunk. He considered the positive responses to be mediated by the direct pyramidal tract.

Prus ('98) was solely interested in the pathways underlying the epileptiform convulsion following strong stimulation of the cortex. He cut one pyramidal tract along with other structures in the internal capsule, peduncle, pons, medulla and the lateral column of the cord and concluded that its interruption in any of these regions did not prevent the appearance of the seizures. Bilateral sections of the tract in the peduncle, pons and medulla were likewise without effect. On the other hand, lesions made in the tegmentum of the midbrain at the level of the inferior colliculi which did not pass deep enough to effect the pyramidal tract abolished the convulsive response, although "isolated movements" remained.

This curious finding has never been confirmed.

By far the most extensive and at the same time completely controlled experiments of this period were done by Hering ('99). He used twenty dogs in acute experiments of many varieties, and found that after section of the pyramids isolated movements could be obtained in the contralateral legs which were somewhat easier to elicit in the hind limbs (13 cm. coil) than in the fore (10 cm. coil). It was also possible to inhibit a contralateral extensor tonus with a weak current. With a current of greater strength cortical epilepsy could be obtained. Hemisections of the medulla made at various levels did not abolish the contralateral movement. He concluded that in addition to the pyramidal tract there must be a "second cortico-fugal path" and that this path must decussate above the medulla. By combining medulla and cord hemisections on different sides he tried to isolate each of these tracts separately. Thus a right medulla hemisection combined with a left cord hemisection (Fig. 3a) isolates the pyramidal tract arising from the left cerebral cortex while a medulla and cord hemisection on the right (Fig. 3b) leaves intact the "second cortico-fugal path" from the right cortex. By these and other methods he determined that not only the pyramidal tract but the "second cortico-fugal path" was capable of mediating both isolated movements and convulsions. The "second path" was found to run with the pyramidal tract in the lateral column. Reference to the figures will show it can be identified with the rubro-spinal tract, as was pointed out by Rothmann.

Rothmann ('01, '02) observed the effect of cortical stimulation on the contralateral limbs after lesions of the pyramidal and rubro-spinal tracts in seventeen dogs.

The pyramidal tracts were cut at their decussation and the rubro-spinal systems were sectioned in the medulla. He found that pyramidal lesions only slightly reduced the excitability of the cortex on the side of the lesion so that, for example, when the coil on the normal side ranged from 10 to 11 cm. that on the damaged side would be around 8 or 9 cm. Lesions of the rubro-spinal tract alone did not affect the response, but combined lesions

from general reasoning that the pathway to the homolateral limb first crossed to the contralateral side with the main descending fibers and then "re-crossed" to the homolateral limb.

Lewaschew in 1885 set this hypothesis to test. He stimulated one motor area and obtained a bilateral response of somewhat different character on the two sides. He then made a left hemisection of the cord at the 12th thoracic level and found

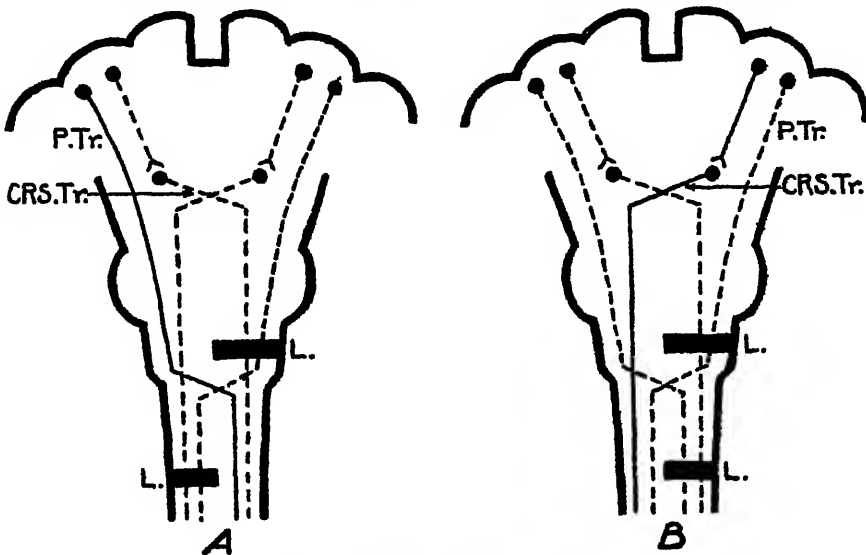


FIG. 3. HERRING'S EXPERIMENTS  
Lettering as for Fig. 1

of the pyramidal and rubro-spinal systems completely removed the reaction.

The homolateral responses in the dog have been studied by Francois Frank and Pitres ('78-'79), Lewaschew ('85) and Wertheimer and Lepage ('96-'97). Francois Frank and Pitres ('78) made kymograph recordings of the movements of both hind legs from stimulation of one motor area and showed that the homolateral response was less energetic and definitely delayed as compared with the contralateral. They did no experimental work to prove their thesis but contended

that on stimulation of the left motor area the homolateral (and contralateral) response was unchanged. He concluded that the pathway to the homolateral hind leg crossed in the pyramidal decussation and then "re-crossed" in the lumbar region (Fig. 4, Tr. A). Stimulation of the right cortex produced no response in the left hindleg but a movement on the right, so there must be, he argued, an alternative recrossing above the 12th thoracic (Fig. 4, Tr. B). He concluded that the hypothesis of Frank and Pitres was correct.

Wertheimer and Lepage ('96-'97) con-

tested these conclusions on the basis of some very ingenious experiments. They made a left hemisection in the medulla above the pyramidal decussation and found that stimulation of the right cortex gave a normal response in the left legs. They then made a left hemisection in the upper cervical region of the cord and found that the left leg movement had

tween the pyramidal decussation and the cervical hemisection, (Fig. 5, "R" Tr.) was removed. What actually happened was that the homolateral movement continued as before. To check the unlikely possibility of a recrossing more cranially they carried the sagittal section forwards through the pons but found that this made no difference to the result. They, therefore, decided against Lewaschew in favor of a direct homolateral tract (Fig.

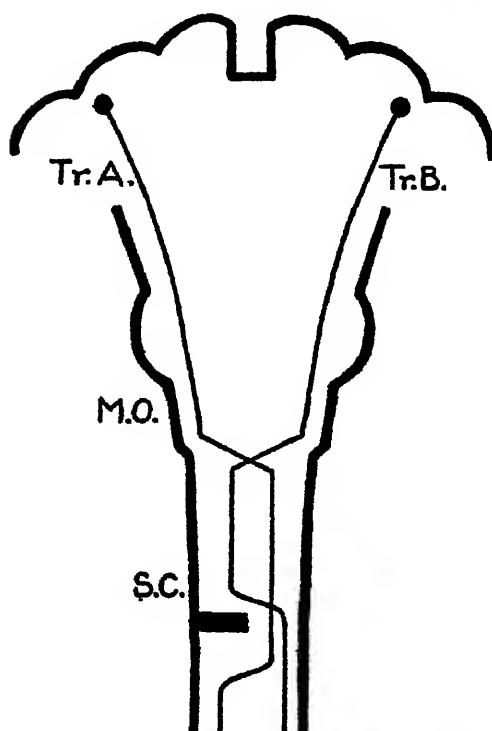


FIG. 4. LEWASCHEW'S EXPERIMENT

Tr.A. and Tr.B.—See text. Other lettering as for Fig. 1.

dropped out and that a right leg (homolateral) movement was now present. They next made a midline sagittal section connecting the two hemisections and sometimes actually removed the intervening block of tissue on the left (Fig. 5). If the recrossing theory was correct, this procedure should obliterate the homolateral movement since the region where the recrossing must take place, i.e., be-

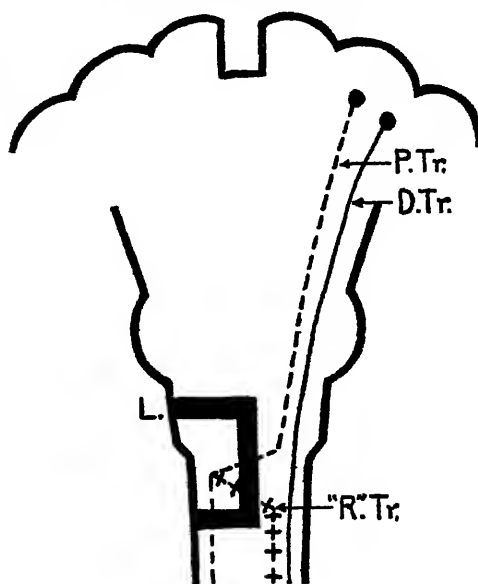


FIG. 5. EXPERIMENTS OF WERTHEIMER AND LEVAGE

D.Tr.—Direct homolateral tract. R.Tr.—recrossed tract of Frank and Pitres and Lewaschew. Other lettering as for Fig. 1.

5, "D" Tr.). They further observed that stimulation of the left motor cortex following a left medulla hemisection above the pyramidal decussation still produced a contralateral response, thus confirming several earlier observers in this respect.

#### EXPERIMENTS ON CATS

The number of investigations on the pathways underlying the response to electrical stimulation of the cortex in the cat

is relatively few. They are reported by Brown-Séquard, Gotch and Horsley, Probst, and Economo and Karplus. The observations of Brown-Séquard have already been discussed.

Gotch and Horsley ('91) investigated the pathways for homolateral movement by a unique method. They transected the spinal cord and then split the caudal end of the oral portion in the midline. Galvanometers were attached to each half so isolated and the electrical changes found in them following stimulation of the motor areas were recorded. They found in the otherwise intact animal a large contralateral and a small homolateral response. The response in the homolateral leg they regarded as being probably mediated through the opposite cerebral hemisphere and cite the following experiment. A right hemisection of the cord was made and a period of 2½ months recovery given. It was then found that in spite of the presence of a direct pathway from the left motor cortex to the left cord (Fig. 6) stimulation of this cortex produced no response on the left side until the current was strong enough to produce bilateral movements. For a complete understanding of this phenomenon the effect of stimulation of the right cortex on the right cord below the hemisection should be known, and it is unfortunately not clear from their report whether this was zero or was merely not observed. The proof of their thesis would require a positive response in this situation, as can easily be shown. Thus in their first experiment (without cord hemisection) the pathway mediating the response on the left side from stimulation of the left motor cortex is assumed to pass first to the right hemisphere and then downwards, "re-crossing" somewhere in its course to the left side. In their second experiment (with a right cord hemisection), since

there is now no response on the left side from the same stimulation, the descending path from the right cortex cannot be the crossed pyramidal tract or the cortico-rubro-spinal system for these are uncut. The tract must, therefore, be one that crosses in this cord below the hemisection (Fig. 6, X. Tr.). But such a path descending on the left side is uncut and should be capable of producing a response on the right side from stimulation of the right motor cortex. Finally, in their one

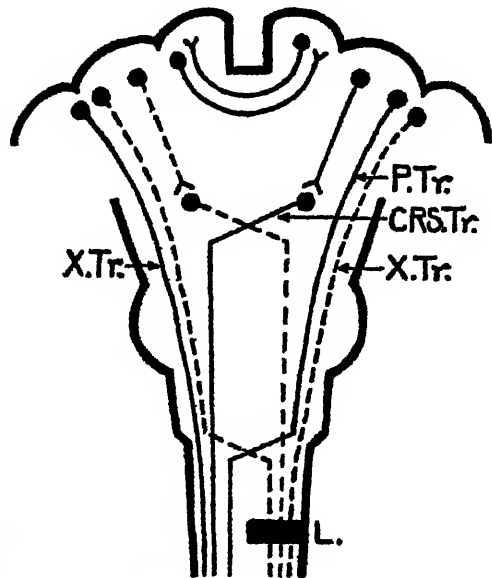


FIG. 6. EXPERIMENTS OF GOTCH AND HORSLEY  
X.Tr.—See text. Other lettering as for Fig. 1

animal in which they removed the cerebral hemisphere opposite to the one stimulated, the homolateral response remained just as large as before.

Probst ('01, '05) made an enormous number of experimental lesions at various levels of the central nervous system, many by means of a special instrument devised by him, the "Hakenkanule." His findings refer to the contralateral response only and are briefly as follows. Complete lesions of the internal capsule abol-

ished all responses from the motor cortex of the same side. Lesions confined to the pyramidal portion of the capsule did not obliterate the reaction but reduced the excitability so that individual movements required a stronger current, epileptiform convulsions an enormous one. Lesions of the thalamus itself also caused a reduced excitability. A complete hemisection of the midbrain cranial to the red nucleus caused a total abolition of the response (Fig. 7a). If only the crus was

except the pyramidal, movements were also possible as stated earlier by Brown-Séquard. Probst finally concluded that both the pyramidal and rubro-spinal tracts were important pathways underlying the contralateral response from stimulation of the motor cortex.

Economo and Karplus ('08-'10) made unilateral and bilateral lesions in the pes pedunculi involving the pyramidal and cortico-pontine tracts. They state that stimulation of the motor cortex on the

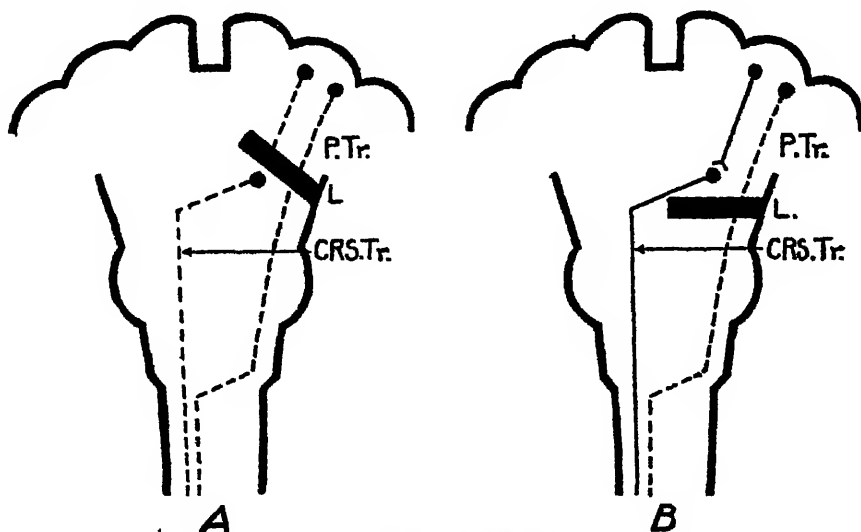


FIG. 7. PROBST'S EXPERIMENTS  
Lettering as for Fig. 1

cut involving the pyramidal and cortico-pontine tracts, but leaving intact "a path to the red nucleus" the reaction was still present although a stronger current was required. A hemisection between the superior and inferior colliculi (Fig. 7b) which left intact the cortico-rubro-spinal system, produced a similar result. Section of both pyramids in the interolivary region of the medulla reduced the excitability but both individual movements and epileptiform convulsions could be obtained. After a section of all descending tracts

side of the lesion produced contralateral movements without the necessity of using more than the normal current. There was no difference in the reactions of the fore and hind limbs, or of the larger and smaller joints.

#### EXPERIMENTS ON MONKEYS

Brown-Séquard states that some of his experiments already mentioned were done on monkeys with presumably similar results to those already reported. In a special article ('87) he described a region

on the callosal gyrus, stimulation of which produced homolateral movements while stimulation of the motor part of the marginal gyrus just above it produced the usual contralateral response. The further course of the homolateral pathways was not determined. Gotch and Horsley's ('91) experiments included monkeys as well as cats, and the results obtained were the same.

Hering ('99) was the first to make carefully controlled pyramidal tract lesions in monkeys. He used eleven macaques and nine baboons in acute experiments. He found, after cutting the pyramids in the medulla after the method of Starlinger, that isolated contralateral movements from stimulation of the motor cortex could no longer be obtained, a result which differs from his findings in dogs. Homolateral movements could be obtained, however, particularly from an area within Brodmann's area 6, which he designated as sulcus X. Occasionally and with a stronger current associated movements of the contralateral hind leg were added to movements of the homolateral limb. An unexpected finding was that in an animal with only one pyramid cut, the homolateral response was easier to elicit on the side of the damaged pyramid than on the intact side.

Probst ('05) reports a case of section of the pyramidal tract in the pons in one monkey in which at the end of three weeks stimulation of the motor area gave isolated movements in the contralateral fingers. In the larger joints no movements could be obtained. He states that pyramidal lesions in the dog and cat only decrease the excitability of the cortex for contralateral movement while in the monkey there is an actual dropping out of whole movements in the larger joints. After hemisection of the midbrain between the superior and inferior colliculi (Fig. 7b)

it was impossible to obtain epileptic convulsions in the contralateral extremities. The presence of the cortico-rubro-spinal system is not adequate for this response in the monkey. Probst confirmed the findings of Hering regarding homolateral movements.

Rothmann ('02) split the pyramidal decussation by the dorsal operation of Magendie in a number of monkeys. He found, after a survival period of two to three weeks, two small areas of excitability in the cortex, one for the fingers and one for the toes. The retention of finger movements is in harmony with Probst's findings, although here the experiment is not crucial since the fibers that do not cross in the pyramidal decussation may have escaped. Rothmann regards the difference between his cases and Hering's animal which gave no response, as due to the period of recovery present in his own cases. A section of the rubro-spinal tract in one animal gave no loss of excitability. Section of both the pyramidal decussation and the rubro-spinal tract, also in one animal, removed most of the cortical excitability including the finger movements. There was retained, however, a rotation movement of the arm which may be due, he says, to the fact that some of the pyramidal fibers escaped.

Economo and Karplus ('08-'10) made lesions in the pes pedunculi in five monkeys. In one of these animals with a complete bilateral section of this structure, stimulation of one motor area produced movements in the contralateral extremities. In the upper extremity the movement occurred in the elbow and in the lower extremity in the foot and toes. The strength of current required is not stated. In the remaining four animals the findings are not conclusive since the lesions were either too large or too small.

## SUMMARY AND CONCLUSIONS

1. In spite of the fact that the term "pyramidal tract" is a very common one, a certain confusion seems to exist as to just what is included in it. A review of the literature shows that it was *defined* by the older experimental anatomists as the sum of those fibers passing through the pyramids of the medulla into the spinal cord, or as equivalent to the total cerebro-spinal system. Definitions which would exclude any cortico-spinal fibers, such as for example fronto-spinal, have no historic sanction. The *conclusion* that the pyramidal tract arises solely from the cyto-architecturally defined motor area or area 4 of Brodmann, is not well established and there is much evidence against it.

2. Complete interruption of the pyramidal tracts without damage to other efferent systems can only be made by section of the pyramids of the medulla, and the experiment to be crucial should be bilateral. This, with survival long enough for observations on recovery, and with adequate anatomical controls, has been reported by only three observers; by Starlinger ('95, '97) in the dog, Schäfer ('10) in the monkey, and Marshall ('33, '34) in the cat. Section of one pyramid alone and of the pyramidal decussation has been reported by a relatively small number of others.

3. The defects in the dog and cat in those cases in which the lesions were more or less confined to the pyramidal tracts were not great and were on the whole less than those found after removal of the motor cortex. This can be most readily seen in the case of the "Berührungsreflexe" of Munk and the contact placing reactions of Rademaker. These reactions are totally and permanently abolished after removal of the motor cortex but are capable of partial recovery following in-

terruption of the pyramidal system. The "extrapyramidal" outflow from the motor cortex is thus shown to be functionally significant.

4. Extensor hypertonus was not found by the earlier experimenters, e.g., Starlinger ('95, '97) and Rothmann ('00-'07) who worked chiefly with dogs. It has been reported by some recent experimenters, e.g., Ranson ('32) and Marshall ('33, '34) in cats. Where it was found it was not great enough to interfere seriously with movement and often needed special postures to bring it out.

5. In monkeys the number of experiments is few and the severity of the defects varied. The attempt of Rothmann ('04) to cut the pyramidal decussation in chimpanzees was without success.

6. The pyramidal tracts have long been regarded as mediating the discrete responses in the limbs from electrical stimulation of the cortex and are now often thought to be the only tracts capable of underlying these reactions. The experimental literature in rabbits, dogs, cats and monkeys is summarized.

7. In rabbits most of the experiments are old and none are found since the turn of the century. Taken at their face value they indicate that the response can appear without the pyramidal tracts, and that of all the fibers mediating the reaction the pyramidal is not even the most important. The interesting if perhaps untrustworthy experiments of Brown-Séquard are summarized and his violent flaying of the physiologists and clinicians of the time who upheld a single localized pathway for the reactions is noted.

8. In the dog and cat a large number of experiments have been made to determine the pathways underlying both the contralateral and homolateral responses from stimulation of one motor cortex. Schiff

('83) was the first to demonstrate that the contralateral discrete response was abolished by section of the lateral column of the cord. Starlinger ('95, '97) clearly showed that section of the pyramidal tract alone was not sufficient to obliterate it. Hering ('99) showed the participation of a "second cortico-fugal tract" which decussated above the medulla. Rothmann ('01, '02) and Probst ('01, '05) showed that this second tract was the rubro-spinal. Probst, and Economo and Karplus ('08-'10) showed that the reaction was present after section of the *pes pedunculi*. The pyramidal tract appears to play a greater rôle in the reaction in the dog and cat than it does in the rabbit and it is also more important than the rubro-spinal system, although the latter is by no means insignificant.

9. An observation of Rothmann in connection with these experiments is of some general importance. Thus he states that section of the pyramidal tracts alone slightly reduces the reaction; section of the rubro-spinal tract has no effect on it whatever; but section of the two together abolishes it completely. In other words, the rubro-spinal tract plays an important rôle, although section of it alone did not show it. Put in general terms, it means that the failure of appearance of any signs of deficit from section of a nerve tract is not proof that the tract does not play a part in the function tested.

10. The investigations on the pathways for homolateral movements in the cat and dog gave conflicting results. The experiments of Wertheimer and Lepage ('96, '97) may be cited as a very ingenious attack on the problem.

11. The experiments in monkeys are relatively few. Hering's ('99) experiments in a large number of animals show

that the response is abolished *immediately* after section of the pyramidal tracts alone. The rubro-spinal tracts are apparently not adequate to mediate the response in those acute experiments. Those who have kept their animals over a survival period of two weeks or more report the presence of some movement. Rothmann ('02) and Probst ('05) in a small number of such animals report the retention of small areas of excitability for the fingers and toes only and Economo and Karplus ('08-'10) report some movements in the larger joints (elbows) in one case.

12. The homolateral response in monkeys is reported by Hering ('99) and Probst ('05) to be easier to elicit from stimulation of the cortex on the side of the damaged pyramid than from that of the sound one. Stated another way, homolateral movements appear more easily when contralateral movements are prevented from occurring. The same phenomenon appears to be present in some of the experiments of Wertheimer and Lepage ('97).

13. Finally, it must be observed that for those who regard the cytoarchitecturally defined motor cortex (area 4 of Brodmann) as the sole site of origin of the pyramidal tracts, any evidence that electrical stimulation of other cortical areas will produce limb movements becomes proof of the "extrapyramidal" mediation of the response. The studies of C. and O. Vogt ('19), Foerster ('31), Bucy ('33), etc., show that the premotor and post-central regions do possess an excitability of a sort, although it differs considerably from that of the motor area. For those who accept the origin of the pyramidal tract given above, e.g., Foerster ('31), this demonstrates that extrapyramidal fibers from these areas can carry out the reaction.



## LIST OF LITERATURE

1. BALLOGHIAN, J. 1879. Beiträge zur Lehre von der Kreuzung der motorischen Innervationswege im Cerebrospinalsystem. *Beiträge zur Anat. u. Physiol. (Eckhard)*, vol. 8, pp. 193-204.
2. BECHTEREW, W. VON. 1909. Die Funktionen der Nervencentra, vol. 2. Gustav Fischer, Jena.
3. BOYCE, R. 1895. A contribution to the study of descending degeneration in the brain and spinal cord, and the seat of origin and paths of conduction of the fits in absinthie epilepsy. *Phil. Trans.*, vol. 186 B, pp. 321-381.
4. BROWN-SÉQUARD, C. E. 1879. Paralytics directes et croisées par lésions de l'encéphale du pont de varoli et de la moelle. *Soc. de Biol. Paris, Compt. Rendus*, pp. 135-137; 139-141; 152-153.
5. —. 1879. Faits montrant que la galvanisation de la surface de chaque hémisphère cérébral agit sur les muscles des membres du côté opposé par deux voies bien distinctes l'une de l'autre. *Soc. de Biol. Paris, Compt. Rendus*, pp. 165-166.
6. —. 1881. Faits montrant que le corps calleux est excitable et qu'il sert en partie à la transmission des excitations galvaniques des prétendus centres psycho-moteurs aux membres. *Soc. de Biol. Paris, Compt. Rendus*, pp. 204-205.
7. —. 1881. Experimental facts showing that the admitted views relating to paralysis of cerebral origin and to the physiology of the so-called motor tract in the brain must be rejected. *Lancet*, vol. 2, pp. 254-255.
8. —. 1882. Faits montrant combien sont variées et nombreuses les voies de communication entre les zones motrices de la surface cérébrale et les membres. *Soc. de Biol. Paris, Compt. Rendus*, pp. 328-332.
9. —. 1887. Sur l'existence dans chacun des hémisphères cérébraux de deux séries de fibres capables d'agir sur les deux moitiés du corps, soit pour y produire des mouvements, soit pour déterminer des phénomènes inhibitoires. *Soc. de Biol. Paris, Compt. Rendus*, pp. 261-264.
10. —. 1889. Recherches cliniques et expérimentales sur les entrecroisements des conducteurs servant aux mouvements volontaires. *Archiv. de physiol. norm. et path.*, pp. 219-245.
11. —. 1889. Expériences montrant combien est grande la dissémination des voies motrices dans le bulbe rachidien. *Archiv. de physiol. norm. et path.*, pp. 606-608.
12. BUCY, P. C. 1933. Electrical excitability and cytoarchitecture of the premotor cortex in monkeys. *Arch. Neurol. and Psychiat.*, vol. 30, pp. 1205-1225.
13. CAMPBELL, A. W. 1905. Histological Studies on the Localization of Cerebral Function. Cambridge Univ. Press.
14. DEJERINE, J. 1901. Anatomie des Centres Nerveux. Tome 2. J. Rueff. Paris.
15. DUPUY, E. 1886. Mouvements musculaires et épilepsie malgré la section du pédoncle cérébral après l'excitation électrique du gyrus sigmoïde du même côté; chez le chien. *Soc. de Biol. Paris, Compt. Rendus*, p. 19.
16. ECONOMO, C. VON, and KARPLUS, V. P. 1908-1909. Pedunculusdurchschneidungen und experimentelle Chorea. *Deutsche Zeitschr. f. Nervenheilk.*, vol. 36, pp. 166-171.
17. —. 1909-10. Zur Physiologie und Anatomie des Mittelhirns. *Arch. f. Psychiat. u. Nervenkrankh.*, vol. 46, pp. 275-356; 377-429.
18. ECONOMO, C. VON, and KOSKINAS, G. N. 1925. Die Cytoarchitektonik der Hirnrinde des erwachsenen Menschen. Julius Springer, Wien und Berlin.
19. EXNER, S. 1881. Zur Kenntnis der motorischen Rindenfelder. *Akad. der Wissensch. Wien, Math.-Naturwiss. Classe, Sitzungsber.*, Bd. 84, Teil 3, pp. 185-190.
20. FLACSAIO, P. 1876. Die Leitungsbahnen im Gehirn und Rückenmark des Menschen. Wilhelm Engelmann. Leipzig.
21. —. 1877-78. Über "Systemerkrankungen" im Rückenmark. *Archiv der Heilkunde*, vol. 18, pp. 101-141; 289-343; 461-484; vol. 19, pp. 53-90; 441-447.
22. —. 1881. Zur Anatomie und Entwicklungsgeschichte der Leitungsbahnen im Grosshirn des Menschen. *Arch. f. Anat. u. Physiol. (Anat. Abth.)*, pp. 12-75.
23. —. 1905. Einige Bemerkungen über die Untersuchungsmethoden der Grosshirnrinde, insbesondere des Menschen. *Archiv f. Anat. u. Physiol. (Anat. Abth.)*, pp. 337-444.
24. —. 1920. Anatomie des menschlichen Gehirns und Rückenmarks aus myelogenetischer Grundlage. Georg Thieme. Leipzig.
25. FOERSTER, O. 1931. The cerebral cortex in man. *Lancet*, vol. 2, pp. 309-312.
26. FRANK, F., and PITRELLI, A. 1878-79. Recherches graphiques sur les mouvements simples et sur les convulsions provoquées par les excitations du cerveau. *Physiologie Expérimentale. Travaux du laboratoire de B. J. Marey*, vol. 4, pp. 413-447.

27. GLIJKY, W. 1876. Über die Wege, auf denen die durch elektrische Reizung der Grosshirnrinde erregten motorischen Thätigkeiten durch das Gehirn hindurch fortgeleitet werden. *Beiträge zur Anat. u. Physiol. (Eckhard)*, vol. 7, pp. 177-188.
28. GOTCH, F., and HORSLEY, V. 1891. On the mammalian nervous system, its functions and their localization determined by an electrical method. *Phil. Trans.*, vol. 181B, pp. 267-326.
29. HERRING, H. E. 1899. Über Grosshirnrindenreizung nach Durchschneidung der Pyramiden oder anderer Theile des centralen Nervensystems mit besonderer Berücksichtigung der Rindenepilepsie. *Wien. klin. Wochenschr.*, vol. 12, pp. 831-837.
30. HOLMES, G., and MAY, P. 1909. On the exact origin of the pyramidal tract in man and other mammals. *Brain*, vol. 32, pp. 1-43.
31. LANGWORTHY, O. R. 1918. The area frontalis of the cerebral cortex of the cat, its minute structure and physiological evidence of its control of the postural reflex. *Johns Hopkins Hosp. Bull.*, vol. 42, pp. 20-60.
32. LEWASCHIEW. 1885. Über die Leitung der Erregung von den Grosshirnhemisphären zu den Extremitäten. *Pflügers Archiv*, vol. 36, pp. 279-285.
33. MAGENDIE, F. 1838. *Précis Élémentaire de Physiologie*. English translation: *An Elementary Treatise on Human Physiology*, by John Revere. Harper and Brothers, N. Y. 1844.
34. MARSHALL, C. 1933. Lesions in the pyramidal tracts in cats. *Proc. Soc. Exper. Biol. and Med.*, vol. 31, pp. 68-70.
35. —. 1934a. Experimental lesions of the pyramidal tracts. *Arch. Neurol. and Psychiat.*, vol. 32, pp. 778-796.
36. —. 1934b. The cortico-fugal pathways mediating the "Berührungsreflex" of Munk and the contact placing reactions of Rademaker. *Amer. Journ. Physiol.*, vol. 109, pp. 178-180.
37. MELLOR, E. L. 1895. Experimental degeneration following unilateral lesions of the cortex cerebri in the bonnet monkey (*Macacus sinicus*). *Proc. Royal Soc. London*, vol. 58, pp. 206-214.
38. MINKOWSKI, M. 1923-24. Étude sur les connexions anatomiques des circonvolutions rolandiques, pariétales et frontales. *Schwiitz. Arch. f. Neurol. u. Psychiat.*, vol. 12, pp. 71-104; vol. 14, pp. 255-278; vol. 15, pp. 97-132.
39. MONAKOW, C. VON. 1905. *Gehirnpathologie*. 2nd ed. Alfred Holder. *Wien*.
40. —. 1914. Die Lokalisation im Grosshirn und der Abbau der Funktion durch korticale Herde. J. F. Bergmann. *Wiesbaden*.
41. MURATOFF, W. 1893. Secundäre Degeneration nach Zerstörung der motorischen Sphäre des Gehirn in Verbindung mit der Frage von der Localisation der Hirnfunctionen. *Arch. f. Anat. u. Physiol. (Anat. Abth.)*, pp. 97-116.
42. PIKE, F. H., C. A. ELSBERG, W. S. McCULLOCH, and A. RIZZOLO. 1929. Some observations on experimentally produced convulsions. The localization of the motor mechanisms from which the typical clonic movements of epilepsy arise. *Amer. Jour. Psychiat.*, vol. 9, pp. 259-283.
43. PIKE, F. H., C. A. ELSBERG, W. S. McCULLOCH, and M. N. CHAPPELL. 1930. The problem of localization in experimentally induced convulsions. *Arch. Neurol. and Psychiat.*, vol. 23, pp. 847-868.
44. PROBST, M. 1901. Über den Hirnmechanismus der Motilität. *Jahrbücher f. Psychiat. u. Neurol.*, vol. 20, pp. 181-291.
45. —. 1905. Weitere Untersuchungen über die Grosshirnfaserung und über Rindenreizversuche nach Ausschaltung verschiedener Leitungsbahnen. *Akad. der Wissensch. Wien. Math.-Naturwiss. Cl., Sitzungsber.*, Bd. 114, Teil 3, pp. 173-312.
46. PRUS, J. 1898. Über die Leitungsbahnen und Pathogenese der Rindenepilepsie. *Wien. klin. Wochenschr.*, vol. 11, pp. 857-863.
47. RANSON, S. W. 1932. Rigidity caused by pyramidal lesions in the cat. *Jour. Comp. Neur.*, vol. 55, pp. 91-97.
48. RANSON, S. W., J. C. MUIR, and F. R. ZHIS. 1932. Extensor tonus after spinal cord lesions in the cat. *Jour. Comp. Neur.*, vol. 54, pp. 13-33.
49. REDLICH, E. 1897. Über die anatomischen Folgeerscheinungen ausgedehnter Exstirpationen der motorischen Rindencentren bei der Katze. *Neurol. Centralbl.*, vol. 16, pp. 818-831.
50. ROTHEMANN, M. 1900. Die Zerstörung der Pyramidenbahnen in der Kreuzung. *Neurol. Centralbl.*, vol. 19, pp. 1055-1061.
51. —. 1901. Über experimentelle Läsionen der Medulla oblongata. *Verhandl. des Congress f. Inn. Med. (1901 Congr.)*, pp. 431-437.
52. —. 1901. Über die functionelle Bedeutung der Pyramidenbahn. *Berlin. klin. Wochenschr.*, vol. 38, pp. 574-579.
53. —. 1902. Die Erregbarkeit der Extremitätenregionen der Hirnrinde nach Ausschaltung cerebrospinaler Bahnen. *Zeitschr. f. klin. Med.*, vol. 44, pp. 183-215.

54. ROTTMANN, M. 1904. Über experimentelle Läsionen der Centralnervensystems beim anthropomorphen Affen (Chimpanse). *Arch. f. Psychiat.*, vol. 38, pp. 1020-1069.
55. —. 1907. Über die physiologische Wertung der corticospinalen (Pyramiden-) Bahn. *Arch. f. Anat. u. Physiol. (Physiol. Abth.)*, pp. 217-275.
56. SCHAFER, E. A. 1900. Textbook of Physiology, vol. 2, p. 778. Young J. Pentland, *Edinburgh and London*.
57. —. 1910. Experiments on the paths taken by volitional impulses passing from the cerebral cortex to the cord; the pyramids and the ventro-lateral descending tracts. *Quart. Jour. Exper. Physiol.*, vol. 3, pp. 355-373.
58. SCHRÖDER, P. 1914. Die vordere Zentralwindung bei Läsionen der Pyramidenbahn und bei amyotrophischer Lateralsklerose. *Monatsschr. f. Psychiat. u. Neurol.*, vol. 35, pp. 1-25.
59. SCHIFF, J. M. 1858-59. Lehrbuch der Physiologie des Menschen. Band 1. Muskel- und Nervenphysiologie, p. 305. M. Schauenburg u. Comp. *Lebr.*
60. —. 1883. Über die Erregbarkeit des Rückenmarks. *Pflügers Archiv*, vol. 30, pp. 199-275.
61. SCHÜLLER, A. 1906. Experimentelle Pyramidendurchschneidung beim Hunde und Affen. *Wien. klin. Wochenschr.*, vol. 19, pp. 57-62.
62. SHERRINGTON, C. S. 1894. Note on experimental degeneration of the pyramidal tract. *Lancet*, vol. 1, p. 265.
63. STARLINGER, J. 1895. Die Durchschneidung beider Pyramiden beim Hunde. *Neurol. Centralbl.*, vol. 14, pp. 390-394.
64. STARLINGER, J. 1897. Die Durchschneidung beider Pyramiden beim Hunde. *Jahrbuch f. Psychiat. u. Neurol.*, vol. 15, pp. 1-42.
65. STEFFAHNY, E. 1888. Zur Untersuchungsmethode über die Topographie der motorischen Innervationswege im Rückenmark der Säugethiere, mit besonderer Rücksicht auf das Halsmark des Kaninchens. *Beiträge zur Anatomie u. Physiologie (Eckhard)*, vol. 12, pp. 41-107.
66. STODDART, W. H. B. 1897. An experimental investigation of the direct pyramidal tract. *Brain*, vol. 20, pp. 441-449.
67. TÖRCK, L. 1851-53. Über secundäre Erkrankungen einzelner Rückenmarksträger und ihrer Fortsetzungen zum Gehirn. *Akad. der Wissensch. Wien, Math.-naturwiss. Class., Sitzungsber.*, vol. 6, pp. 288-312; vol. 11, pp. 93-119.
68. VOLT, O. 1906. Über strukturelle Hirncentra, mit besonderer Berücksichtigung der strukturellen Felder des Cortex pallii. *Anat. Anzeiger*, vol. 29, (Suppl.) pp. 74-114.
69. VOLT, C. and O. 1919. Allgemeinere Ergebnisse unserer Hirnforschung. *Jour. f. Psychol. u. Neurol.*, vol. 25, pp. 279-464.
70. WERTHEIMER, E., and LEPAGE, L. 1896. Sur les fonctions des pyramides bulbaires. *Arch. de physiol. norm. et path.*, pp. 614-621.
71. —. 1897. Sur les mouvements des membres produits par l'excitation de l'hémisphère cérébral du côté correspondant. *Arch. de physiol. norm. et path.*, vol. 9, pp. 168-180.

### ADDENDUM

Since the submission of this paper to press, a number of contributions to the subject have been made by various authors. Kennard ('35) and E. C. Hoff ('35) have advanced further evidence confirming the idea already expressed that the pyramidal tract arises from a more extensive cortical area than the primary motor cortex or area 4 of Brodmann. Kennard demonstrated by the Marchi technique, that removal of the premotor area (area 6 of Brodmann) of the monkey causes a definite cortico-spinal degeneration. Some of the degenerating fibers descend directly from area 6; others

first pass backward through the cortex to area 4 and then descend. E. C. Hoff by the method of *bouton* degeneration came to the same conclusions. On the other hand, Levine and Poliak, in a paper read before the American Neurological Association, could find little evidence of any significant cortico-spinal degeneration from lesions of the premotor area.

The functions of the pyramidal tract have been studied by section of the pyramid in the medulla by Barron in the rat, by Tower in the cat, and by Tower and Hines in the monkey.

In the rat Barron ('34) found disorders

in posture, in gait and in the grasp in the contralateral limbs—the forelimbs suffering more than the hind. There was a paresis in the toes and a decrease in “flexor tone.” The affected foreleg was extended with difficulty at the elbow joint, and it was often misplaced, so that it crossed the opposite foreleg, or was placed on the dorsum of the foot. The gait improved rapidly, but the power of grasp returned slowly and never fully reached the normal. The placing and “postural adjustment reactions” of Rade-maker were initially absent, and showed no recovery during the survival period of the animal (a maximum of sixty days). Electrical stimulation of the cortex after the lesion gave no response when tested with the bipolar method. With unipolar stimulation, no flexor responses could be elicited, but extensor movements could be obtained. On the intact side, the preponderance of responses was flexor. The conclusion was drawn that the pyramidal tract “is chiefly concerned with the regulation of flexor movements of the fore limbs, especially of the digits and manus.”

In the cat Tower ('35) found disorders in gait, in posture, and in the placing and hopping reactions. The observations on tone deserve special consideration for the conclusion is reached, in contrast to those of Ranson and Marshall, that “the basic postural mechanism of extension is intact, symmetrical and not overactive.” Certain signs which superficially might give the appearance of extensor hypertonus were admittedly present. Thus, in the gait the extremities were used “stiffly with little or none of the characteristic triple flexion,” there developed a “circumduction . . . resembling that of a hemiplegic man,” and “in running and jumping the stiffness was frequently so great as to throw the animal towards the nor-

mal side.” Extensor postures were not infrequently maintained when the normal extremities had flexed. The knee jerk “was larger and longer enduring than on the normal side, and occasionally this leg retained a residue of the extension. Yet if the animal relaxed during examination the difference between the sides diminished, until on the verge of sleep the jerks became symmetrical, and both of the loose type previously characteristic of the side opposite the lesion.” In the supine position, little or no resistance was encountered on passive flexion.

The interpretation placed by Tower on the phenomena of extension noted above, is that they are dependent upon a “deficiency of flexor activity.” Thus the extensor postures appear “as a normal extension abnormally prolonged because of a deficiency in flexor activity.” The apparent overactivity of the extensors in the knee jerk is “due to the operation of active flexion in checking the normal jerk and the lack of such flexion on the incompletely innervated side.” The conclusion is drawn that “the lack of clonus in the post-operative syndrome and of a clasp knife phenomenon, indeed the conspicuous absence of all signs of spasticity, together with the very moderate resistance to passive movement, sufficiently demonstrated that severing the pyramid had not increased the excitability of the spinal extensor centers as does the hemiplegic lesion in man.”

The findings on cortical stimulation were interesting, and it is stated that posture placed a most decisive rôle in the results. In the supine position, stimulation of the intact side, produced first a relaxation of a pre-existing extensor tonus (presumably the result of the anesthetic) and secondly, with a little stronger current, an active flexion. On the affected side, relaxation (inhibition) of the exten-

sor tonus could be produced, but active flexion was never obtained. In the prone position in one animal "the lateral border of the anterior sigmoid gyrus gave a curious slow retraction and flexion of the opposite forelimb, and that was all." It is not clear from the report what were the findings in the prone position in the other animals, and if both the prone and supine positions were used in the same animals.

As a final conclusion it is stated that the experiment shows that the excitability and inhibitory components of cortical activity are dissociated at some pre-spinal level; that the excitatory component travels along the cortico-spinal tract; and that the inhibitory component descends to the cord along other pathways. In criticism one may question (1) whether the extensor phenomena can be satisfactorily explained away as a deficiency of flexor activity, and (2) whether the thesis of excitation-inhibition dissociation as formulated by the author is proved by the experiment. The data as given are not sufficient to permit an accurate analysis of all the complex factors involved. The findings on inhibition, moreover, are in part confirmed

and in part denied by the recent extensive investigations of Rioch and Rosenblueth ('35) on the subject. That there is a difference between the phenomena resulting from motor area removal and pyramidal section is unquestioned,—such differences have been commented upon by every investigator who has compared the two lesions. But whether these differences are dependent upon a fundamental excitation-inhibition dissociation may be very seriously doubted.

Tower and Hines ('35) in a preliminary report state that section of the pyramid in the monkey produces a syndrome similar to, but graver than that found in the cat, again without spasticity. Stimulation of the motor, premotor and prefrontal areas (especially the premotor) following the pyramidal lesion causes a "release" of tonic closure of the fingers into a grasp. The fine type of movement characteristic of the normal motor cortex can no longer be obtained, but the larger so-called adverse movement may be elicited, as can Jacksonian seizures. No comment is made by the authors as to whether the excitation-inhibition dissociation is considered as applying in the monkey.

#### ADDITIONAL LITERATURE

- BARRON, DONALD H. 1934 The results of unilateral pyramidal section in the rat. *Journ. Comp. Neurol.*, vol. 60, pp. 45-56.
- HOFF, E. C. 1935 Corticospinal fibers arising in the premotor area of the monkey. *Arch. Neurol. and Psychiat.*, vol. 33, pp. 687-696.
- KENNARD, MARGARET A. 1935 Corticospinal fibers arising in the premotor area of the monkey. *Arch. Neurol. and Psychiat.*, vol. 33, pp. 698-710.
- RIOCH, D. MCK. AND A. ROSENBLUETH 1935 Inhibition from the cerebral cortex. *Amer. Jour. Physiol.*, vol. 113, pp. 663-676.
- TOWER, SARAH S. 1935 The dissociation of cortical excitation from cortical inhibition by pyramidal section, and the syndrome of that lesion in the cat. *Brain*, vol. 58, pp. 238-255.
- TOWER, S. S. AND M. HINES 1935 Dissociation of the pyramidal and extrapyramidal functions of the frontal lobe. *Science*, vol. 82, p. 376.



# THE GENE, ITS FUNCTION AND ITS MEANING IN GENETICS

By DR. W. F. H. STRÖER

*Anatomical-Embryological Laboratory, Groningen, Holland*

THIS study will only be a critical survey of the theory of the gene, that is, the theory of the genetical units. These units, the genes, are, according to some authors, thought to form the atoms of organization. According to this conception the genes would be the activators of all the processes of life, even of the most fundamental ones, which result in the totality that we call an organism.

Goldschmidt (1928, p. 308) says that "die Gene Glieder eines Systems sind, nämlich der Eizelle mit Kern und Plasma am Ausgangspunkt und des gesamten Keims an jedem weiteren Punkt der Entwicklung."

In this study we will discuss the function and structure of the gene in relation to the problem of organization and test the facts on which these hypotheses of the atomistic structure of life are founded.

## HISTORICAL SURVEY

We will give here only a short review of the history of the above mentioned conception. The "physiological units" of Spencer form its origin; however, it was Darwin, with his "provisional hypothesis of pangenesis" (1868), who laid the foundation of all later hypotheses. Studies on the genetic behavior of plants and animals but even more the general facts of biology, for instance, regeneration, sex, development, induced him to this.

According to him each living creature is "a little microcosm, a little universe, formed of a host of self-propagating

organisms, inconceivably minute and as numerous as the stars in heaven" (p. 404). "Each animal and plant may be compared to a bed of mould full of seeds, most of which soon germinate, some lie for a period dormant, whilst others perish" (p. 404).

The influence of Darwin's hypothesis was enormous and we see that many researchers adopted this way of looking at the structure of the organism. In their excellent study Délagé and Goldsmith say: "Toutes les théories modernes qui lui (hypothesis of Darwin) ont emprunté l'idée de particules représentative, n'ont rien ajouté d'essentiel aux explications proposées par elle." Only de Vries forms an exception. De Vries (1889) localized his units, the "pangenes," in the nucleus of every cell. There they are supposed to be inactive, but at a certain moment leave their place of origin, to go into the protoplasm, to activate this.

All these hypotheses culminate in Weismann's "Determinantenlehre." Weismann invented an elaborate and ingenious system of units of different order. The conceptions of the different authors were united by him into one logical system, which was based on the units of de Vries formed in the nucleus, and Naegeli's division of the organism.

With Naegeli, he divided every organism into two parts, *viz.* two kinds of protoplasm, the idioplasm, which was to serve for propagation and possessed all genetic and organizing properties and the trophoplasm, which was to perish when

the organism died. Furthermore he invented units of different order, for instance the "determinants," which determined the different processes. These were units of higher order, formed by the biophores, which were united into ids, and the latter into idants, which were identical with the chromosomes in the nucleus.

If we see in Darwin the founder of the atomistic conception, we must regard Weismann as the man who enlarged it into the system which was to play such an important rôle in experimental biology, that is, not only in genetics, but also in experimental embryology. Two lines of research derive from Weismann. These are of different order; the first is a physiological, the second a morphological one. We will discuss them separately. The physiological one depends on the belief that development and organization are the result of a sum of processes and that every single process is determined by some factor, Weismann's determinant, the gene in genetics. The morphological conception depends on Weismann's systematic orders of units in the chromosome. Authors have tried to catalogue the whole organism in his chromosome-set. They tried to refer every character to the nuclei and believed that then they knew the structure of organization and life. They forgot, however, Goethe's phrase "Fehlt leider nur das geistige Band." But only the latter is responsible for organization and life.

#### THE MORPHOLOGICAL CONCEPTION OF THE GENE

As we have mentioned already, this conception of the gene is to be traced back in history to Darwin. Schaxel (1922) has pointed out that two principles of genetics are derived from Darwin's work: 1. the historical conception of life with the different consecutive generations. 2. the

atomistic view of the organism, which is conceived to be an "Eigenschaftsaggregat." Both principles are in some way or other to be found in modern genetic conceptions, though many researchers do not actually stick to them (Johannsen, Correns, Woltereck and others). Yet there is not such a great difference between the original conception of Darwin and the modern researchers. Darwin thought that in the whole organism there were corpuscles responsible for the forming of the organs, whereas several modern researchers, in imitation of de Vries and Weismann, are of the opinion that only that part which is responsible for development and organization possesses these units. From a unit of organism the gene has become a unit of organization. De Vries' conception "Einzeleigenschaft" has played an important rôle (cf. Johannsen for criticism, p. 406). This point of view is for the greater part based on Mendel's laws, which taught that the different characters were inherited apart from each other. Eventual deviations could easily be explained by cytological researches (e.g. crossing-over phenomena). Starting from linkage and crossing-over, conceptions too well-known to be discussed here, the school of Morgan has made chromosome-maps for *Drosophila*. In these maps they tried to catalogue the whole organism or rather its characters, symbolized by its genes, like the books of a library in the index-system.

However important and interesting these researches may be, they have not led us any further as regards insight into the nature of life and organization. Moreover there are various difficulties on which we will touch but slightly.

Morgan's chromosome-map is based, as mentioned, on the phenomena of linkage and crossing-over. The explanation for

this was seen in a breaking of the chromosomes. Winkler pointed out the possibility of another explanation, by his "Konversionstheorie," according to which special factors could be converted. In that case it would not be necessary to assume any breaking of the chromosomes in order to explain these phenomena. Stern opposed Winkler's suggestion to the utmost of his power and produced all sorts of proofs in favor of Morgan's theory. Yet Winkler is not convinced and believes that both explanations hold good.

It is interesting indeed that still other methods have been applied to make a chromosome-map; Muller and Painter (1932) did this when they made a map of the x-chromosome of *Drosophila*. Muller started from the consideration that there was "a lesser frequency of crossing-over, when the genes appeared more crowded" in the chromosome. With the aid of x-rays he could show that there were not only differences in cross-over frequency, but also in mutation-frequency in the different regions of the chromosomes. By means of x-rays he had formerly been able to ascertain in the x-chromosome different spots where it was broken. In order to determine the place in the x-chromosome where the boundary between the two regions lies, that is, between the break-line C and the factor "bar," he assumed that "the physical size of the remainder of the active region to the right of this line is proportional to the frequency of mutation to the right of bar (in comparison with these respective values to left of bar)" (p. 352). The map thus obtained agreed with the real size, found by deletion. By deletion we understand the breaking of a chromosome under the influence of x-rays, after which the remaining parts stick together and an eliminated part sticks to another chromosome. By measuring such deleted

chromosomes Muller and Painter could estimate approximately the real distance of factors in the chromosome and thus come to an exact location of these factors.

However, objections can be raised against this "deletion-method." Sturtevant and Schultz (1931) pointed out that it is possible that the x-rays have not only a breaking influence, but also can induce mutation. The occurrence of unknown subgenes in deleted chromosomes points to this.

Muller and Painter found so-called "inert regions" in the x-chromosome in the same manner as was known in the y-chromosome, that is, spots where no factors were present. They think that the x-chromosome originated from a translocation; its right half would be identical with the left half of the y-chromosome, which was connected with the left half of the x-chromosome by a translocation after deletion. The authors account for the inert part by a degeneration process of the genes. On the other hand one might think that in this case the genes have not been formed (cf. below) and that here the more fundamental organizing processes take place.

In this section there should also be a short discussion of some attempts to subdivide the genes. This point of view is similar to that of Weismann with his system of units of different order. Only a short discussion of the "subgene-hypothesis" of the school of Serebrowsky and Thompson's "side-chain theory" will be given. Both served to explain the phenomena of allelomorphism. The Russian researchers started from the so-called "Treppenallele," which were found in the factor "scute" in *Drosophila*. The subgenes which were responsible for these results were "treppenartig" situated in the chromosome (fig. 1). Different objections have been raised to this hypoth-



esis, of which those of Sturtevant and Schultz (1931) seem to us the most important. Agol (1932) had pointed out as a convincing proof that new subgenes appeared with a "deleted" chromosome. We have already mentioned the possibility that we here have to do with an induced mutation. Moreover as Bridges pointed out for the factor "plexus" and Sturtevant and Schultz (1931) for "scute," the properties of the genes depend on the spatial relations which they bear to other genes in the complex ("the dominance of any one gene is a function of the system as a whole"). However, Brink (1932) did not find such an influence in maize. He believes the genes to form groups. With deletion, the chromosomes would in the

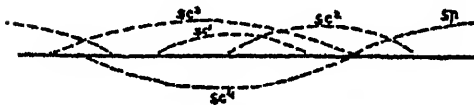


FIG. 1. SERIES OF STEP ALLELOMORPHS  
Sc³, Sc², Sc¹, Sc⁰, Sp. (Agol, 1932)

case of maize break between two groups, in *Drosophila* within one group.

These spatial relations of the genes are altered with deletion, which argues against Agol's view. Moreover the threshold value plays a part as Sturtevant and Schultz could prove for "achaete" and "scute." The latter influences the development of the brushes of *Drosophila* only when "hairless" is present (that is, when the threshold-value is reached).

The subgene-hypothesis is no longer in the center of interest. Dubinin (1932) abandoned the hypothesis and now there is only Agol as the courageous, but unconvincing defender.

Thompson has put forward his side-chain theory to account for the phenomena of multiple-allelomorphism; according to him (1925 and 1931) the gene consists of

"a main particle firmly anchored in the chromosome with varying numbers of one or more kinds of other particles attached." The first are called "protosomes," the second "episomes." Mutations would mostly arise from loss, sometimes from increase of one of the episomes.

It is difficult to give one's opinion on this hypothesis; this cannot be done until more is known about multiple allelomorphism.

Finally we wish to remind our readers that just as Weismann united his biophores into determinants and ids, other researchers have done this too, e.g., Plate in his Erbstockshypothese (1925) in order to explain the phenomena of development and organization (cf. below). Friesen (1932) tries something similar with his theory of the "Kettenmutationen" (cf. below).

Herewith we finish our exposition of the morphological conception of the gene, to return to it in the discussion of the organization.

#### THE PHYSIOLOGICAL CONCEPTION

In connection with the well-known researches in physiology and experimental embryology the geneticists have tried to determine the structure and function of the gene. This way of looking upon the matter joined up with the data from experimental embryology, that is, both geneticists and embryologists tried to project back the cause of all kinds of phenomena to a material basis.

As the geneticists thought of this basis as being in the genes localized in the nucleus of the cells, so the embryologists saw it in special parts of the eggs of embryos in the so-called "organ forming substances." These are of such great importance that Penner (1925) has proved that only the cells with pole-plasm (containing the organ forming substances) can

form a germ-band, whereas the other parts of the eggs are not able to do so. Schleip (1927) even maintains that in all probability the above-mentioned can be applied in the case of all animals where the spiral cleaving type occurs (Polychaeta, etc). However, the animal pole-plasm behaves differently in those forms which have a trochophora during development from those without a larval stage.

It seems difficult to us to pronounce an opinion on this; however, this is easier for the so-called "organizer" in the development of amphibian eggs and especially of the eggs of the Urodela. If we go more deeply into this subject it is to show how the ideas of organization and induction which originally seemed to give the fundamental solution of development, in the end have not led us any further but that they have been the cause of a great number of fine and important researches.

Spemann was the first to discover that the chorda-mesoderm-plate was able to induce the ectoderm, which in a normal case would have produced skin, to form a neural plate (secondary) with sense organs; the organizer often differentiated itself into chorda and myotomes and then an intestine was formed. So there arose a more or less complete secondary organism (organization). With later researches it has been proved that the neural plate or parts of the central nervous system were able to do the same.

Through this a severe shock was given to the implicit belief in the organizer. Researches by Goertler and others into which we cannot go here, have largely contributed to this, as they taught that the ectoderm was not nullipotent but totipotent. Apparently the induction process does not serve to "induce" something new, but to regulate the processes of development and to conduct them

in some special direction or other. Of late years this opinion has taken firmer root through the frequency and multifariousness of the organizing bodies and processes. We shall mention only a few of them; differences in temperature (Gilchrist, 1928), killed parts of embryos, neural plate and chordamesoderm plate (Spemann and pupils), cancer and muscular tissue (Hampe, see Woerdeman, 1933), and the most varying parts of amphibian embryos (Holtfreter, 1933).

Of late a hypothesis of Woerdeman's that glycolysis plays an important rôle in the process of induction has come to the foreground. Fischer and Wehmeier (1933) thought that glycogen is the induction matter; Woerdeman wants the process "glycolysis" to play a part. However, Waddington and J. and D. Needham and also Holtfreter maintain that it would be a substance with lipoid character. However this may be it is of less importance to us. Woerdeman writes: "Der Induktor hätte als Ausgabe durch seinen eigenen Stoffwechsel die physikalischen und chemischen Milieuveränderungen hervorzurufen, wodurch die physicochemischen Differenzierungen des Reaktionssystems in eine gewisse Richtung gelenkt werden."

We have gone into this question rather elaborately, because many geneticists see an agreement between the working of the organizer and the genes. Originally both were looked upon as chemical substances which have an important influence on development.

The opinion that the genes are enzymes can be traced back to Driesch. According to others they are autocatalyzers. An important expansion was only possible when Goldschmidt in imitation of Hagedoorn, developed his nowadays so important physiological theory of heredity according to which the genes are quantities of hormone and enzyme. According

to this theory the gene would only be an autocatalytic substance-particle of not only a definite quality, but also of a definite quantity. The gene now is put in action when the suitable substrate is present, and determines the result of a reaction. The development of an organism, according to Goldschmidt, can be resolved into a number of chain-reactions with an organ forming substance for everyone of them, which determines the differentiation. This conception is the result of a great number of genetical and experimental researches which were made

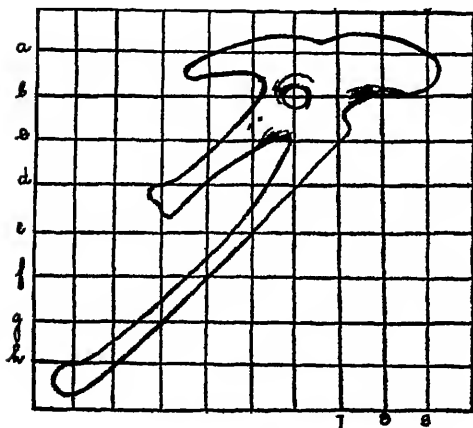


FIG. 2. PELVIS OF ARCHAEOPTERYX

by Goldschmidt and his pupils. At the same time we wish to recall to mind the fine researches of Huxley and his co-operators; the researches on *Lymantria* and *Gammarus* form the most important work in this respect. We are of the opinion that a discussion of these well-known researches is redundant. Huxley has further been able to explain phenomena from palaeontology and the relationship of animals on the basis of the work of d'Arcy Thompson. The latter drew complete animals or special organs in a square lattice-work; by deforming this lattice-work in different directions he obtained

forms of kindred animals or the shape of the organs in kindred species of animals (cf. figs. 2 and 3, on the pelvis of *Archaeopteryx* and *Apatornis*.) The cause of this, as d'Arcy Thompson (1915) had already remarked, lay in an "increase or decrease in some or more of the actual and relative velocities of growth" (cf. de Beer, 1930). Huxley pointed to the connection with the working of the genes, as these have a similar influence.

However, it follows that the genes do not "determine" the development and the differentiation, but only "control," in other words, conduct in a definite direction (cf. below). We become more

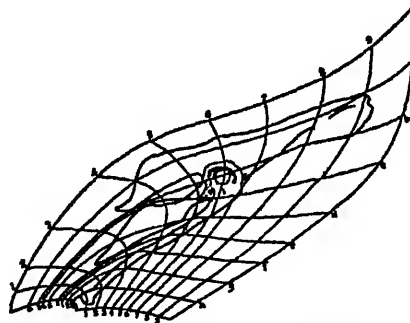


FIG. 3. PELVIS OF APATORNIS

convinced of this conception through some modern researches.

Lillie and Juhn (1931) studied the physiology of the development of the breast- and saddle-feathers of the brown Leghorn fowl, that is, the influence of thyroxine and the female sex-hormone on the design of the feathers. They found that smaller quantities gave an axial design and larger quantities caused stripes throughout the whole feather or designs along the edge. So these researches argue in favor of the view that the above-mentioned hormones play an integrating part in the origin of feather designs. Against this, objections have been raised

by Danforth (1933) who thought that the genetic constitution of the animals experimented upon had an important influence on the results. He therefore repeated these experiments with animals with different genetic constitutions and noticed that he had been right. Danforth maintains that "it is primarily the tissues and not the hormone which determine the effect." Montalenti, a pupil of Lillie, found in the Plymouth Rock fowl that the barred pattern results from the co-operation of both genetical and physiological (intermediate hormone-acting) factors (*J. Exp. Zool.*, 69: 269). This is in harmony with the lack of "Nachwirkung" of a hormone, as the investigations of Kemp (1933) on a recessive dwarf stock of the mouse illustrate. This abnormality is the result of an insufficient action of the pituitary, as could be demonstrated by transplantation of this organ of a normal individual into a dwarf which then became normal in size. If the latter was crossed with a genetically normal individual dwarfism reappeared in the children ( $F_2$ ).

The best way to express the importance of genes is by quoting the words of Huxley and de Beer (1934): "While the genes are by themselves incapable of initiating the processes of development and differentiation, it is obvious that they play an active part in the control of these processes, once development has been started and their presence is essential" (p. 403).

So we see that in experimental embryology as well as in genetics attention is once more drawn to the cause of organization, the nature of which is still unknown to us, in spite of the many attempts made to understand and to explain it. (cf. below).

This section must not be concluded

without pointing to the fact that objections have been raised to the conception that the genes are hormones.

Contrary to the conception of quantity of hormone, defended by Goldschmidt, Fisher has remarked that this is incompatible with the results of crosses between the allelomorphs of one gene. The products of such a cross, the so-called "compounds," should always be intermediate and dominance of one allelomorph over another should never show itself, as has been observed. Apparently other factors besides differences of quantity play a part in this case. The problem of multiple allelomorphs has by no means been solved, as Plate remarked. Inexplicable under Goldschmidt's conception is the discovery of Timoféeff-Ressovsky (1932) that in the case of *Drosophila* different allelomorphs already known could be obtained by means of x-raying from the gene white and that these could be converted into each other, e.g., eosin blood, etc.

The conception that the genes are hormones has also been objected to. Various physiologists doubt the exactness of the hormones and believe that nerves serve for the conduction of the stimuli. It is not possible to express an opinion in this matter; we only point out that Kondratjew (1933) considers the genes to be the total of the electro-magnetic fields and rays, emitted by nucleo-proteids of the nucleus. This conception, however, is not based on researches, but only on deductions and hypotheses, lacking a convincing foundation. We mention it for the sake of completeness only.

Without having striven after any completeness at all, we believe that nevertheless we have put forward and discussed some important points about the physiology of the gene in this section.

## THE PROBLEM OF ORGANIZATION

In the introduction it was mentioned that some geneticists regard the organism only as an "Eigenschaftsaggregat." Yet this point of view is not accepted by all researchers. The organism is not the result of a summing-up of characters, in the same way as a more highly organized, "celly" individual is a colony of protists, for in both cases we have to do with a unity, a totality. It is difficult, if not impossible (Lubosch) to give a definition of the idea "organization," but we may describe it as a harmonious coöperation of the different parts of an organism, which on the one hand are to some extent independent of each other, but on the other hand are subject to the influence of the whole.

These phenomena prevented most geneticists from accepting the "Eigenschaftsaggregats" hypothesis as correct; as did also those characters which were the result of different genes and most of all the heredity of the organization characters, which did not follow the laws of Mendel. The difference between the latter and the ordinary mendelizing characters (cf. below Rensch) was difficult to explain with the aid of the atomistic conception. Some authors tried to explain it by means of quantitative differences. According to them the heredity of stature in man and of racing capacity in the thoroughbred horse is not the result of one or of a few genes, but of a thousand. Other researchers did not believe in such a simple explanation and tried to save as much as possible with the aid of different subsidiary hypotheses or to find a new manner of explanation.

The difference between simple and organizing characters has been the cause of several dualistic hypotheses. All researchers agree in localizing the first in

the chromosomes; but they place the latter either in the nucleus or in the protoplasm.

Friesen (1932) proposed the theory of "Kettenmutationen." It was assumed that during a mutation a row of genes mutated simultaneously, but that the only observable effect was caused by both end genes of this row. This hypothesis was proposed to explain the simultaneous occurrence of changes in eye-color and fertility in the different allelomorphs of the gene "white" in *Drosophila*.

This hypothesis has little or nothing to do with the explanation of organization, but it forms the starting point of a possible manner of explanation, that is if we regard such a chain of mutations as a unit of higher order, as Plate (Erbstockhypothese) did. He calls them "Radikale." From the chromosomes they may go into the achromatin of the nucleus, where the so-called "Erbstock" is localized. The last-mentioned is responsible for the organization characters, for as Plate observes we know many genes which influence in some way or other the development of a limb but none which produce its development. The gene "apterous" in *Drosophila* forms a possible exception. In the silkworm a wingless mutant is known which possesses characteristic pupal wing-pockets into which in a normal individual the wing-rudiment projects, which of course does not occur in the wingless form. This makes it probable that we have to do here with a factor which influences the wing development in a negative sense. These organization characters are bound to the ground plan of development. For this reason, other researchers believe them to originate in the protoplasm (Correns, Castle, Philipptchenko and many others). That the latter plays a part in heredity is certain. East (*Am. Nat.* 68: 289) in his

critical survey of this subject, is not convinced of this. Jollos (1933) reviewed the different arguments for it. Most important is the often observed fact that the products of a cross differ from those of the reciprocal cross. (Goldschmidt, Kühn for animals; F. Wettstein, Correns, Michaelis and many others for plants).

The experiments on inheritance in the gastropod *Limnaea peregra* of Boycott, Diver, Garstang and Turner demonstrated the influence of the protoplasm on the heredity of the spiral coil of the body and shell-lefthandedness or righthandedness.

These points demonstrate a certain influence of the protoplasm, but they do not prove that the organization characters are bound to it alone. Recently Hämmerling (1931, 1932) studied this point in *Acetabularia* experimentally. Young denucleated individuals could to some extent develop, but the result was closely related to the stage of development at which they were denucleated. Miss van Herwerden (1932) has rightly pointed to the possibility of an after-effect of the nucleus, which might play a part. Such an influence cannot be eliminated; for this reason we believe an *experimentum crucis* to be difficult, if not impossible.

All these reasons make us sceptical as to the dualistic conception of the hereditary factors which divide the organism into two parts, a central one formed by the archaic organization characters, surrounded by a layer of mendelizing characters (cf. Woltreck, 1934). Where can we draw an exact line between these two? There is no such line; for those characters which are the distinctions of the subspecies in one form are the characteristics of families and orders in related forms (cf. Rensch, 1933). The facts referred to by Jollos do not prove that hereditary characters are bound to the protoplasm, e.g. the well-known "Dauermodifika-

tionen" with Woltreck's interesting experiments on *Daphnia cucullata* in Lake Nemi as illustration. They only prove a certain "influence" of the protoplasm on the result of the processes of development and organization.

Jollos thinks the occurrence of directed mutations in *Drosophila* of great theoretical significance. The results of Timoféeff-Ressovskiy are contrary to them. They cannot explain orthogenetic series, for Jollos worked only with allelomorphs, and not with species and families, as in palaeontology (cf. Plate, 1932). So Castle (1934) cannot convince us that only factors in the protoplasm can explain the genetic result concerning "size-inheritance" and "sex-control"; for a simple explanation with ordinary mendelizing characters is satisfactory (cf. Green, Spöttel, 1932). Fortuyn (*Genetica*, 16, 321) described a case of mendelian segregation of quantitative characters between tribes of mice, which were closely related. The effect of blending-inheritance should result from the action of modifiers in crosses between tribes with many genetical differences.

From a theoretical point of view it is clear that the protoplasm influences the action of a gene. If we accept the genes to be units of some physical or chemical constellation, found (that is, localized) in the nucleus, they must pass into the protoplasm to activate it, as de Vries has described. So it is obvious that the processes resulting from the coöperation of gene and plasm depend on the structure of the latter; this can easily be demonstrated by the well-known influence of different temperatures on the flower colors in *Primula sinensis*. In the living cell with its continually varying processes (respiration, pH, etc.), there exists a continually changing chemical and physical plasmatic basis. This is important; for the moments

of originating and action, and the time between these two points are so different for the genes in one organism, that we can distinguish some groups in relation to these differences (Haldane, 1932). It is clear that the structure of the protoplasm alters the developmental influence of a gene, even as this originates in the nucleus. The dualism, cell-protoplasm, is not a primary one, for both form a unity, the so-called "Stammsystem" of Cohen-Kysper (1933), or the "matrix" of Woltereck (Crustacea-researches, 1934). The experiments which showed that the distribution of chemical particles in the egg, in some animals, has no important influence on development and organization, support this view. When the original distribution is altered by centrifuging the chief processes of development, such as blastulation and gastrulation, are to a large extent normal (sea-urchin, Lyon; *Cumingia* and *Arbacia*, Morgan and Spooner; *Rana*, Gurwitsch.) This could account for the fact that an influence of the protoplasm or genetic results is in relatively few cases observed; on the other hand, it is not right to believe that the matrix, the spermovium, is our last basis of knowledge, and that all investigations on the influence of cytology on heredity are worthless. The atomistic conception has led us astray. According to Jennings "there is indeed no such thing as a unit character and it would be a step in advance if that expression should disappear."

Yet we believe that it is possible to maintain the genes and their significance, provided we do not start our theoretical assumptions from the genes, but from the organism itself. The genes must not be looked upon as the physiological atoms of the organism, but as its products which play a part in its support and development. They should not be regarded as present in the same form, from the incip-

ient stage of development, but only in a potential form.

This view is closely related to the most modern investigations and suppositions in experimental embryology, in which it is demonstrated that the young embryo should be looked upon as a totality in which all characters are potentially present. Yet the development is led by a factor, that is: "the original control of differentiation in all cases appears to be exerted in relation to what may be called a biological or morphogenetic field." (Huxley and de Beer, p. 274). In the beginning there is only one field, but as development advances, it is subdivided into sub-fields, each of which controls the development of a certain part or organ of the embryo. Then there is a mosaic of fields (limbs, eye, etc.). This subdivision goes on constantly. According to Gurwitsch (1930) there is in every biological process a factor, which can be compared to the field. Every stage in such a process is a function of time and of this constant parameter, that is, the inherent invariant of the organism. Gurwitsch and his collaborators have shown that this can be applied to several kinds of processes in the development and function of animals and plants.

A short description of Anikin's investigations (1929) on the morphotrophic field of the formation of the chondral anlagen of limbs will be given. This field controls the shape of the nuclei of the mesenchyme cells. The forces acting on the surface of the nuclei radiate from the origin of the field (Feldquelle); the latter is situated in the axis of the anlage. The vectors in this field are inversely proportional to the distance between their origin and the origin of the field. With the aid of this simple law, Anikin was able to predict the shape of a nucleus at every distance from the field-origin. As

figures 4 and 5 show theoretical and real shape agree in every way.

This constant factor which forms the morphogenetic field in the embryo is the gene in the adult.

Now there are several difficulties, e.g. this factor is not a chemical substance, but has a physical structure as Gurwitsch showed. Many researchers think the genes to be hormones (Goldschmidt, Huxley, and many others); but the hormones are not the cause of the organization, they only control it. Chemical substances play, of course, an important part, e.g. the mitogenetic substance

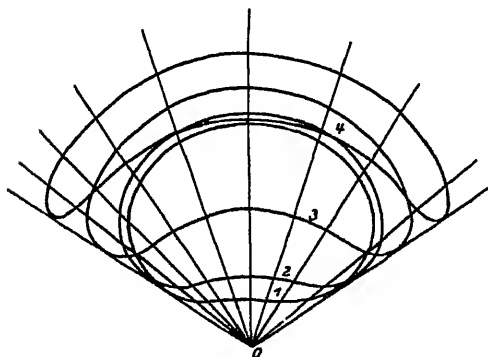


FIG. 4. THE FORM OF THE NUCLEI, AS A FUNCTION OF THE DISTANCE BETWEEN ORIGIN (O) AND NUCLEUS

through the formation of the mitogenetic rays (Gurwitsch).

It is premature to discuss the structure of the gene with our imperfect knowledge of this subject, but it is very important to conceive the organism as a whole and not as a colony of genes.

The former point of view has many advantages over the latter. It makes clear that different characters can be influenced by one gene or factor (polymere factors, many examples in teratology and pathology). O. Vogt's "dysnomic variability" (1929) agrees with it. Vogt and his collaborators found that the variability of characters was bound to a certain pattern (e.g. the spots on the

wing-cases in beetles). They invented an intricate terminology with several kinds of variability of which the so-called "Kombinationsdysnomien" are important for phylogeny and pathology. We find a connection with heredity in "das 'Muster' ist im Genotypus fester begründet als seine Ausdehnung." Anatomical variations show us many examples of this principle. It is a well-known fact that, in most cases when there is somewhere a muscle variation in an individual, we observe in the same body-area of the other side a muscle variation which is not

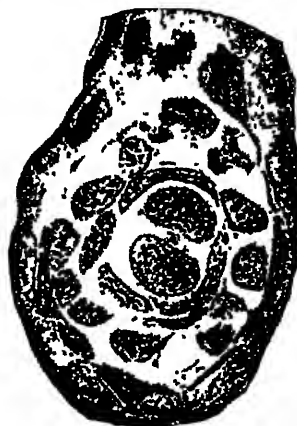


FIG. 5. SECTION THROUGH THE ANLAGE OF A PHALANX OF TRITON

strictly identical with the first one. Another example may be found in the researches of Buschke (1934), who studied the ossification in the bones of twins, triplets, etc. in man, with the aid of x-rays. He could distinguish two groups of ossification-centers, a first one which follows canonic rules and is typical of the different families and a second one which does not show this regularity and varies most individually. There are plenty of other examples in anatomy and embryology. The adoption of fields superposed on each other is applied with success to some problems in neurology.



Lastly we recall to mind the above-mentioned fact that Muller and Painter found inert regions in the x-chromosomes. It is possible that there are localized here the causes of processes, which should not have been split up into genes, and should be of a higher order, e.g., the cause of the organization.

We gave a brief description of the possibility of a genetic organic conception. It would be characterized by a variant on the well-known sentence of du Bary: "die Pflanze bildet Zellen, nicht die Zelle bildet Pflanzen," as "the organism forms the genes, and not the gene the organism."

This synthetic view is gaining ground in many branches of biological science. In this article, especially in this section, we have tried to show that in genetics, too, such an organic conception is possible. It not only brings the facts into a

better relation to each other but can also deepen and enlarge our insight into many problems.

#### CONCLUSION

In this article we have tried to give a discussion of the value of the gene in genetics, with quotation of some modern ideas and investigations on its morphological and physiological significance. We have tried to look upon the gene as a part of a totality and to subordinate it in an organic conception of the living creature.

At this place I wish to acknowledge my indebtedness to the criticism of Professors J. C. H. de Meyere (Amsterdam) and T. Tammes (Groningen) who were so kind as to read the manuscript of this article. Last, but not least I thank Professor de Buriat, not only for his kindness in allowing me to finish this article, but more than that for his constructive judgment.

#### LIST OF LITERATURE

- ANTKIN, A. W. 1929. Das morphogene Feld der Entwicklung. *Roux' Archiv Entwmech.*, 114: 545.
- AGOL, J. J. 1931. Step-allelomorphism in *Drosophila melanogaster*. *Genetics*, 16: 254.
- . 1932. Das Sichtbarmachen der verborgenen Allelomorphen Scute-Teile mit Hilfe von Faktorenausfällen (deficiencies). *Biol. Zbl.*, 52: 349.
- BEER, G. R. DE. 1930. Embryology and Evolution. *Oxford*.
- BOYCOTT, A. E., and C. DIVER. 1923. On the inheritance of sinistrality in *Limnaea peregra*. *Proc. Royal Soc. Ser. B.*, 95: 207.
- BRINK, R. A. 1932. Are the chromosomes aggregates of groups of physiologically interdependent genes? *Am. Nat.*, 66: 444.
- BUSCHKE, F. 1934. Röntgenologische Untersuchungen an menschlichen Zwillingen und Mehrlingen. *Fortschr. Geb. Röntgenstrahlen. Leipzig*.
- CASTLE, W. E. 1933. The gene theory in relation to blending inheritance. *Nat. Ac. Sc.*, 19: 1011.
- . 1934. Possible cytoplasmic as well as chromosomal control of sex in haploid males. *Nat. Acad., Sc.*, 20: 101.
- . 1934. Size inheritance in rabbits: Further data on the back-cross of the small race. *J. exp. Zool.*, 67: 105.
- COHEN-KYSER, A. 1933. Die Bedeutung des Gens für Determination und Entwicklung. *Naturwissenschaften*, 21: 229.
- CORRENS, C. 1928. Über nichtmendelnde Vererbung. *Z. ind. Abst. lebre. Sup.*, 1: 165.
- DANFORTH, C. H. 1933. Genetic factors in the response of feather follicles to thyroxin and theelin. *J. exp. Zool.*, 65: 183.
- DARWIN, CH. 1868. Animals and Plants under Domestication II.
- DÉLAGE, Y., et GOLDSMITH. 1916. Les Théories de l'Évolution.
- DUBININ, N., und H. FRIEDEN. 1932. Die Unmöglichkeit einer Erklärung des Falls der Treppenaltele Scute vom Standpunkt der Goldschmidtschen physiologischen Theorie der Vererbung. *Biol. Zbl.*, 52: 147.
- FISHER, R. A. 1932. The evolutionary modification of genetic phenomena. *Verh. 6. Internat. Kongr. Vererbgsu.*, 1: 165.
- GILCHRIST, F. G. 1928. The effect of a horizontal temperature gradient on the development of the egg of the urodele, *Triturus torosus*. *Phys. Zool.*, 1: 231.
- GOLDSCHMIDT, R. Einführung in die Vererbungswissenschaft, 5te Auflage.

- GOLDSCHMIDT, R. 1931. Die entwicklungsphysiologische Erklärung des Falls der sogenannten Treppenallelomorphe des Gens von *Drosophila*. *Biol. Zbl.*, 51: 507.
- GREEN, C. V. 1933. Further evidence of linkage in size inheritance. *Am. Nat.*, 47: 377.
- GURWITZ, A. 1930. Die histologischen Grundlagen der Biologie, 2te Auflage.
- HALDANE, J. B. S. 1932. The time of action of genes, and its bearing on some evolutionary problems. *Am. Nat.*, 66.
- HÄNDLERLING, J. 1931. Entwicklung und Formbildungsvermögen von *Acartularia mediterranea* I. *Biol. Zbl.*, 51: 633.
- . 1932. Idem, II. *Biol. Zbl.*, 52: 42.
- HERWERDEN, H. W. VAN. 1932. Het Organisme in Wording.
- HOLTFRSTER, J. 1933. Nachweis der Induktionsfähigkeit abgetöteter Keimteile. Isolations- und Transplantationsversuche. *Roux' Arch.*, 128: 584.
- HUXLEY, J. S., and G. R. DE BRER. 1934. The Elements of Experimental Embryology. *Cambridge*.
- JOHANNSEN. 1926. Elemente der exakten Erbkheitslehre, 3te Auflage.
- JOLLOS, V. 1931. Genetik und Evolutionsproblem. *Zool. Anz. Sup.*, 5: 252.
- KEMP, T. 1933. Hereditary dwarfism in the mouse. *Acta Path. Scand. Sup.*, 16: 189.
- KONDRATJEW, N. 1933. Über die Natur der Korrelationen bei den Wirbeltieren. *Brg. Anat.*, 30: 419.
- LILLIE, F. R., and M. JOHN. 1932. The physiology of development of feathers I. Growth-rate and pattern in the individual feather. *Physiol. Zool.*, 1: 124.
- MULLER, H. J., and T. S. PAINTER. 1932. The differentiation of the sex chromosomes of *Drosophila* into genetically active and inert regions. *Zschr. ind. Abstlebre.*, 62: 316.
- PLATE, L. 1927. Lamarckismus und Erbstockhypothese. *Z. ind. Abstlebre.*, 43: 100.
- . 1932. Genetik und Abstammungslehre. *Z. ind. Abstlebre.*, 62: 47.
- REINCH, B. 1933. Zoologische Systematik und Artbildungsproblem. *Zool. Anz. Sup.*, 6: 19.
- SCHAKEL, J. 1922. Grundzüge der Theorienbildung in der Biologie, 2te Auflage.
- SCHLEIP, W. 1927. Entwicklungsmechanik und Vererbung bei Tieren. *Handbuch d. Vererbgslehre.*, Lief. 1, IIIA.
- SPELMANN, H., F. G. FISCHER und RISE WEEDMAYER. 1933. Fortgesetzte Versuche zur Analyse der Induktionsmittel in der Embryonalentwicklung. *Naturwissenschaften*, 1933: 305.
- SPÖTTEL, W. 1932. Ein Beitrag zur Vererbung der Körperformen und des Skeletts. *Züchtungskunde*, 7: 296.
- STERN, C. 1930. Multiple Allelie. *Handbuch d. Vererbgs.*, IG Lief. 1, IIIA.
- . 1932. On the occurrence of translocations and autosomal non-disjunction in *Drosophila melanogaster*. *Nat. Acad. Sc.*, 20: 36.
- STURTEVANT, A. H., and J. SCHULTZ. 1931. The inadequacy of the subgene hypothesis of the nature of the acute allelomorphs of *Drosophila*. *Nat. Acad. Sc.*, 17: 265.
- THOMPSON, D'A. 1915. Morphology and Mathematics. *Royal Acad. Edinburgh*, 1915.
- THOMPSON, D. H. 1931. The side-chain theory of the structure of the gene. *Genetics*, 16: 267.
- TIMOFEEFF-REMOVSKY, N. W. 1932. Mutations of the gene in different directions. *Proc. 6th Internat. Congr. Genet. Ithaca*, 1: 308.
- VOGT, C., and O. VOGT. 1929. Hirnforschung und Genetik. *J. Psych. New.* 39: 438.
- VOGT, O., and S. R. ZARAFKIN. 1929. Über dynamische Variabilität und ihre nosologische Bedeutung. *J. Psych. New.*, 39: 447.
- VRIES, H. DE, 1889. Intracellular Pangenesis.
- WEISMANN, A. 1904. Vorträge über Descendenztheorie.
- WADDINGTON, C. H., J. NEEDHAM and D. M. NEEDHAM. 1933. Physico-chemical experiments on the amphibian organiser. *Nature*, 1933.
- WINKLER, H. 1932. Konversions-Theorie und Austausch-Theorie. *Biol. Zbl.*, 52.
- WOLKEDMAN, M. W. 1933. Über die chemischen Prozesse bei der embryonalen Induktion. *Proc. Kon. Acad. Wet. Amsterdam*, 36: 842.
- WOLTERBECK, R. 1934. Artdifferenzierung (insbesondere Gestaltänderung) bei Cladoceren. *Ber. X. Jahresvers. Göttingen (6-9 Sept. 1933)*: 12.



## PROBLEMS IN THE CLASSIFICATION OF NEONATE ACTIVITIES

By KARL C. PRATT

*Central State Teachers College, Mt. Pleasant, Michigan*

### INTRODUCTION

THE study of the behavior of the newborn infant has assumed an ever increasing significance during the past score of years, as biologists, psychologists and educators have striven to differentiate the instinctive from the acquired and the maturational from the learned components of human behavior. The almost insuperable difficulties encountered in attempts to effect such a separation on the adult level originally directed attention to a stage of human development wherein it was thought that all types of activity must be innate or unlearned. It was believed that an inventory of the response repertory of the newborn child would result in a catalogue or list of the raw materials from whence the adult was envisaged as arising under the influence of the environment as architect and builder. It was conceded by some writers that certain response patterns of an innate character were not to be observed at birth, but emerged at later times when the appropriate structures of the organism had matured. Others contended that even these activities were present, though in imperfect form, in the newborn baby.

The era of the biographic or diary method of determining the nature of *Homo sapiens* at birth, and his subsequent development, extended approximately from 1780 to 1910. One of the earliest and keenest biographers was Tiedemann (48), whose work gave rise to a long line of

infant biographies. The greatest of all such studies was made by Preyer (40) upon his children. So accurate and unbiassed were his observations that the volumes are still of value for reference purposes. Other important biographies or diaries were made by Darwin (13), Shinn (43) and Lowden (25). The latter has had an ill-deserved obscurity.

In these biographies we may discern the rudiments of later techniques of study and of the problems which further investigators have set themselves. The early pioneers in the field of infant psychology sought to determine the instinctive and reflex endowment of human beings; they attempted to relate its manifestations to the phylogenetic past, and to trace the sequential or genetic changes from birth to childhood, or to the adult stage.

The earlier contributions differ from those made by the investigators during the past score of years in that the biographers formulated their conclusions upon the observation of a limited number of children, usually one, sometimes two, and most frequently upon their own children or those of near relatives. The reliability of their generalizations was also vitiated by their dependence upon qualitative observation and report rather than upon an instrumentalized technique for the automatic registration or recording of behavior manifestations. Their experimentation was exceedingly crude, and neither variations in type nor gradations in the intensity of external stimuli were measured or controlled. Lastly, they

failed to develop suitable systems of classification which would have enabled them to digest their accumulated data and to understand the significance of such integration.

The first major experimental study of human neonates was undertaken by Canestrini (8). Employing a method that had been suggested in connection with Bechterew's (2) recommendations for the objective study of infants, he measured the effects of different types and intensities of external stimuli upon the respiration and circulation of newborn infants, automatically recording changes in these indices by means of the pneumograph, special tambours, and the kymograph. In this manner the effects of external stimuli upon two continuing vegetative activities were objectively measured. The classification of the effects is hence limited to the respiratory and circulatory consequences of stimulation, and is effected with reference to the modality of the stimulus and the nature of the sense-organs which were stimulated.

Following closely upon Canestrini's work, Benedict and Talbot (3) published their important investigations upon the metabolism of newborn infants. The metabolic indices provided evidence of activity changes of the organism, as did the crib-recorder records obtained by these workers on the periodicity of general motility. It is indeed unfortunate that for almost two decades this important contribution escaped the attention of practically all psychologists. The objective study and analysis of the nature of the human infant would have been furthered immensely if this work had been more widely known.

As it happened, the greatest impetus in the English-speaking world to a renewed and intensive examination of the neonate equipment was provided by the scanty and

relatively haphazard experimentation of Watson (50) and his associate Blanton (6); work which served as the point of departure for intense and vigorous controversy upon the nature and number of innate instincts and emotions. Watson sought to determine their number as a basis for subsequent behavior manifestations to be induced largely by environmental conditioning. His service to child psychology in challenging the uniqueness and innateness of a host of instincts and emotions limited, for the most part, by nothing more than the possibilities of our vocabulary, cannot be overlooked, even though some of his generalizations and experimental findings have been unconfirmed or have proven inadequate.

The criterion of the innateness of behavior, namely, its presence at birth, did not remain unchallenged. There developed a desire to learn the antecedents of the neonate repertory, in other words there was a demand that the history of particular responses be chronicled from their fetal beginnings. Preyer was a pioneer in this field, but the first comprehensive studies of prenatal development were carried out by Minkowski (28) (29), and the ablest review of the history of such investigations of fetal behavior has been written by Carmichael (10). Minkowski, by qualitative methods investigated the reactions of fetuses delivered by Caesarean section when abnormal maternal conditions necessitated the termination of pregnancy. In this way he was able to trace the genesis of particular responses in relation to the maturation of the nervous system. At about the same period Bersot (4) (5) made an intensive sequential study of the plantar response in man, and employed statistical devices to express its changing manifestations and variability.

From these researches it has become

apparent that the old conception of fixed, discrete reflexes must be abandoned in favor of the view that the early stages of human behavior show, not specificity, but generalization; and that specificity of function comes as the result of individuation through growth processes and through environmental modifications. At first the number of action segments brought into play by stimulation of most sense-organs is very great. An 'action segment' of the organism is, in most instances, a moveable part whose boundaries are the points of articulation. Thus the leg as a whole is a gross segment subdivided into a number of smaller segments. With progressive maturation the stimulogenous zones tend to become smaller and the responses to be more restricted or localized.

In the previous century it became apparent that there exists in the infant a definite order of development along various axes of the body. Buck (7) and others observed what they termed a development from "fundamental to accessory" in the responses of the body segments. In the present century this has received experimental confirmation in many investigations upon lower animals by Coghill (12) and his associates, and it is now termed the 'proximo-distal course of growth.' The direction of growth along the major axis of the body—the cephalo-caudal—has also received considerable attention. These axial trends of development in human beings have been studied by Irwin (22) (24), Shirley (44), and Marquis (27). Shirley has built up a sequential or genetic classification upon this foundation and its implications for general psychology have been expressed by Goodenough (18).

The research program initiated by Weiss and his associates Pratt, Nelson, and Sun (39), Irwin (21), and Marquis (26) embodied a frontal attack upon the major problems of neonate development. New

and improved techniques were devised to give objective records and to control the conditions of stimulation.

An analysis of the researches in infant psychology during the past twenty years indicates a need for more systematic classifications of the known responses of the newborn child if a better understanding of the neonate organism is to be attained. With few exceptions the summaries of behavior at this developmental stage embody mixed principles of classification: some responses are classified according to stimulus and receptor loci; some with respect to whether they are innate or acquired; others according to their effects or purposes; and some with reference to their developmental aspects, antecedent and subsequent. Frequently the classification represents primarily an enumeration or a cataloguing of responses. The summaries of Blanton (6) and Dennis (14) illustrate the latter type; both writers classify largely according to the site of movements. The summary by Hurlock (20) is still less systematized.

It would appear self-evident that a given summary should employ some consistent principle of selection and organization. The basis used must depend upon the aim of the particular inventory; indeed, no one mode of classification will serve all purposes.

In the succeeding portion of this article an attempt will be made to outline the principal systems of classification, to state the contribution made by each to the understanding of the newborn organism, and to portray the advantages and disadvantages of any particular set of categories.

#### CLASSIFICATION ACCORDING TO STIMULI AND SENSE-ORGANS

One of the oldest and commonest systems of classification of human behavior

makes use of the various modes of energy which serve as stimuli, and utilizes the sense organs as fixed reference points. Physiology and psychology alike have utilized this scheme. The summaries by Peiper (31) and by Pratt (33) are type examples of it in the field of neonate behavior.

The major advantage of this type of classification is that its reference points are relatively well-defined and constant. The stimulus may undergo certain fluctuations or modifications but the sense organ remains a stable reference point. This makes it feasible to pass from a point in one cross-sectional plane in the developmental continuum to the same point in a preceding or succeeding cross-section, and thus to effect a comparison between the behavior at different levels of development.

As an illustration, we may present a stimulus of a certain intensity and wavelength to the visual sense-organs at the late fetal or early neonatal level and thus evoke circulatory and respiratory changes, blinking (visuopalpebral reflexes), pupillary reflexes and frequently Moro's Umklammerung or clasp reflex (a complex response involving a start or jerk of the body and an extension and abduction of the extremities followed by flexion and adduction), and like responses. Later, during the cross-section of the suckling stage, the same stimulating conditions fail to release the Moro response; in fact persistence of this response has a pathological significance. At a still later period of development (at about 5 years C. A.) a new response has appeared and the child, if English-speaking, may say "red." And again, the time may come when the same individual when confronted by this stimulating condition, considerably modified, will put his feet on the clutch and brake pedals of the automobile he is driving. In

the latter cross-sections the new responses mentioned must be learned responses even though a definite degree of maturation was prerequisite for such acquisition.

The constant reference points and the ease with which the classification is made on this basis have contributed to its extensive use and still commend it. It lends itself readily to normative *sampling* and is therefore excellent for clinical purposes.

The major defect of such a system is that it tends to stress isolated, part activities and stimulus-receptor aspects rather than the *integrated* organism in action.

#### CLASSIFICATION ACCORDING TO ONTOGENETIC CAUSAL FACTORS: MATURATIONAL VS. ENVIRONMENTAL

For the educator the differentiation of nature from nurture, of the innate from the acquired forms of behavior has, mistakenly perhaps, assumed transcendent importance. One may incline towards the predeterminism of a Morgan (30) or the epigenesis of a Child (11). In child psychology the two extremes are exemplified by Gesell (15) and Watson (51). The latter holds that the characteristics of a given individual are the result of combinations and organizations of innate behavior produced by environmental factors. Gesell would assign the secondary rôle to the environment for he maintains that it is the nature of the organism which determines or sets the limits of possible environmental modifications of the organism.

The attempt to distinguish the unlearned from the acquired forms of behavior has led to a continuous ontogenetic regression in the search for innate behavior. At first, presence at birth served as the chief criterion, then the reference time was pushed back into the prenatal

stage and still there arose critics such as Givler (17) who pointed out that even in the prenatal environment the possibilities of exercise and learning could not be ignored.

Gesell and Thompson (16) attacked the problem by means of the 'co-twin control,' the assumption being that identical twins present the same possibilities of behavior, and that if heredity and maturation are most important the twins should have the same type of responses even though their environments are different. This seems to be an unimpregnable position but Richards and Irwin (41) have questioned the assumption that identical twins are completely 'identical' and from the other angle one may ask whether the environmental differences are significant. Perhaps we are only witnessing the consequences of Child's 'standard environment' when we observe the behavior repertory of the newborn infant.

In the light of these difficulties the value of a classification in terms of 'innate' or 'acquired' becomes dubious indeed. An illustration will serve to show that crucial experimentation will be necessary before any given response may properly be classified under these categories. The newborn infant does not possess a protective wink reflex to the approach of an object to the eyes, but at about 60 days of age such a reflex makes its appearance. Is it the result of maturation or is it a learned response? Watson held to the last-mentioned possibility, and indeed this seems quite plausible when one notes that the requisite factors for the establishment of a conditioned response are present. These are: a stimulus which does arouse the response in question (contact stimuli provided by the infant's hands touching the eye-lids, lashes, etc. and causing the lids to close) preceded by visual stimuli from the approaching hands. Further repeti-

tions of this sequence eventually result in the response of winking to the approach of an object. This explanation seems at first to be satisfactory and yet there are animals which have such protective wink reflexes at birth with no possibility for such a process of conditioning in the fetal stage.

Among classifications of innate reflexes Warren (49) has given one of the most compact.

#### TELEOLOGICAL CLASSIFICATIONS

Closely allied historically to the view that responses may profitably be classified as innate or acquired is the belief that they may be divided into those which are purposive, i.e., which effect certain results upon the organism or upon the environment and in general work towards maintaining the integrity of the individual, and into those which serve no apparent ends. This, therefore, gives rise to a classification of responses in terms of their effects rather than in terms of reference to organismic factors either genetic or topographical in nature.

There are a number of telic rubrics of which the oldest and most widely used is one which interprets responses in terms of their utility as mechanisms of defense or protection. When a particular response in the ontogenetic present can be so classified only with strained logic a solution is sought by referring the teleological consequences to the phyletic past. For this reason the doctrine of recapitulation is almost invariably linked with the notion of the purposive character of neonate behavior.

Basically a defense response consists of one of two types of movement with reference to the external stimulating situations: (1) repelling the stimulating source and (2) withdrawing from it. When the movements are very ineffective, as objec-

tive examination often finds them, their telcological functions are supposedly manifested in the *intent* of the movements rather than in their *execution*.

A few responses of the newborn infant will serve to illustrate the criteria for such a classification and to make apparent some of its glaring weaknesses. First, let us consider certain responses which have been definitely termed movements of defense. Watson (50) reports that holding an infant's nose will arouse the emotion of 'rage,' and that some of the movements involved are defensive in character. The results obtained by Pratt, Nelson, and Sun (39) from such stimulation fail to support Watson's findings as to the existence of a general, emotional pattern of response. True, there is a relatively limited amount of movement on the part of the trunk and limbs in a few cases, but the prevailing mode of reaction is an arching of the back and a backward movement of the head. Theoretically this response might be considered defensive, in that its "intent" is to withdraw from the source of stimulation. However, such an interpretation in no way accounts for movements of the head in one particular direction rather than in another. Movement from side to side would be just as useful. Still more purposeful would be definite movements of the hands towards the nose.

The Shermans (42) have stated that a firm pressure exerted upon the chin releases defense responses which are characterized by movements of the arms and hands, so that the experimenter's finger is touched. They report that the efficiency is not high at first, but that it improves rapidly with increase in age. The experiment should be repeated, with better controls, for the writer has been unable to confirm it in experimentation upon quiescent infants.

With respect to the bending back of the

head it is interesting to observe that stimulation of the forehead by a cold temperature cylinder, or of the eyes by a flash of light (Peiper's *Augenreflex auf den Hals*) will all produce the same reaction, namely, a withdrawal or attempted withdrawal from the source of stimulation.

Akin to these are the pupillary reflexes, the *Rückgrat* (Galant) and abdominal reflexes, and the visuopalpebral or blinking response. All of these appear plausible as protective reflexes, but we must stretch the point greatly if the cochlear-palpebral response is to be interpreted as "defensive." Recourse must be had to phylogenetic history if such responses are to be fitted into the present category.

Other responses of protective nature, if viewed as atavisms, are the grasping reflex and Moro's clasp reflex (as elicited by jarring, loss of support, and similar stimuli). These are alleged to have had a survival utility in an arboreal past of the human race.

Lastly, the plantar response has been alleged to be a movement of defense. Babinski (1) has claimed that not only is the triple retraction of foot, leg and thigh 'defensive through withdrawal,' but that the plantar flexion of the toes during the first hours after birth is defensive, in that it represents a *counter-offensive*. The subsequent events are strange indeed, for thereafter the toes show plantar extension upon plantar stimulation, and the response must now be 'defensive by withdrawal.' Still later, at about the age of one year, the toe response is again one of flexion (counter-attack). This example, as well as others which could be cited, suffices to cast doubt upon the value of the term, 'defense reflex,' as a descriptive category in the classification of neonate behavior.

Additional evidence (36) which militates against the term 'defensive' as ap-



plied to the plantar response is obtained if one varies the site of stimulation and observes the effects, if any, upon the aroused responses. Stimulation of the plantar surface of the foot in the traditional fashion evokes a flexion of the foot, and hence brings a withdrawal of the member from the source of stimulation. Now, if the top (dorsum) of the foot is stimulated in the median line, the consequence is again a flexion of the foot at the ankle—but in this case the foot does not move away from the stimulus but rather maintains contact with it. So without altering the response we change its character of 'defense by *withdrawal*' to 'defense by *attack*' by merely changing the site of stimulation! The allegedly defensive features of many reflexes will probably bear scrutiny no more successfully than does the plantar response.

Inasmuch as certain responses do perform somewhat recognizable rôles in the life economy of the child, classifications such as the vegetative must be entertained. The utility of responses which participate in the basic activity of alimentation is granted by hypothesis. It is slightly more difficult to discover any maintenance value in some of the respiratory and circulatory changes which are brought about through external stimulation.

Thus far we have evaluated the 'purposive' behavior; now we turn to the 'non-purposive.' For the newborn infant the item which is usually entered under this heading is the 'random' or 'spontaneous' activity. However, these teleological terms came into use when the nature of such behavior was undetermined. Thanks to the researches of Benedict and Talbot (3), of Carlson and Ginsburg (9), Taylor (47), and Irwin (23) we are now beginning to have insight into this aspect of behavior and can interpret it in pur-

posive terms just as successfully as we may interpret the more specific responses. The necessary conditions for this normal 'random' activity are either external, such as continued thermal or noxious stimuli, or internal, developing from changes which take place along the alimentary tract. Talbot (46) considers the general activity consequent to lowered environmental temperatures to be a type of temperature-regulating mechanism. This being true, the activity may be considered directly purposive in a vegetative sense. Yet when we consider the same behavior as an accompaniment of hunger contractions of the stomach, there is nothing of immediate telic value to be discerned. Of course, as a 'drive' manifestation, the increased activity may be attributed a phylogenetic though not an ontogenetic value. Further, one may term it 'purposive' because of the effects that it may exert upon the social environment.

Notwithstanding all of this, it is very doubtful whether much is to be gained by attempting a teleological classification of neonate behavior. The 'present utility' of a response may be of great importance and interest, but can well be treated in other and in more satisfactorily based types of classification.

#### CLASSIFICATION ACCORDING TO DEVELOPMENTAL CHARACTERISTICS OF RESPONSES

In theoretical (35) and experimental (36) (37) (38) papers the writer has attempted to develop a system of classification which will portray behavior changes in their organismic setting. He believes that the sequential pursuit of certain responses is only a partial approach to a truly genetic psychology, and is in its way just as arbitrary and fractionated as is a stimulus-receptor classification. Norms may be established for manipulation,

locomotion, speech, and the like, but the individual then appears as a conglomeration of different streams of action.

The writer agrees with Bersot (5) that responses which are considered apart from the remainder of the behavior of an organism must then lose their principal significance. How, then, may human behavior be classified so as to present adequately its present, past, and future interrelations? What type of classification will sweep through and include such phenomena as the sequential development of particular responses; the individuation of behavior along the various axes of the organism; the changes in the reflexogenous zones; and changes in the types and range of stimuli, in the case of learning, of fatigue, and in the responses which occur under different physiological states and under pathological conditions?

In spite of certain difficulties it seems feasible to classify behavior as 'specific' or as 'generalized' in respect to other responses in the same cross-sectional (i.e., at the same age level) plane, or in respect to its preceding or succeeding phase in the longitudinal (i.e., at different age levels) plane.

Obviously such relativity precludes a simple division of responses into two groups. Actually, what is required is a quantitative expression of stimulus-receptor-effector relations at different age levels and under various physiological conditions of the organism. When this is accomplished we shall have expressed the varying degrees of 'specificity' of the response repertory of the infant. It will then be easy to determine whether one response is more 'specific' than another by comparing their respective places in our table of quantitative values. Some may object that such a classification stresses the quantitative features but neglects the qualitative aspects such as the type and se-

quential order of participation of action segments in a response. In reply it may be said that what we have termed the quantitative features manifest a fairly definite order of development whereas those we have termed 'qualitative' appear almost saltatory or emergent in character. For example, the change from plantar flexion to plantar extension of the toes. It is true that there is a transitional stage, but the transition period is marked by the appearance of *either* flexion *or* extension. The same action segments are involved but the character of movement varies according to the nature of the innervation. But this fact need not be lost sight of, in our classification of activities, even though it cannot be equated quantitatively. The difficulty here is that our analysis of movements stops short at action segments rather than muscle groups and, more important still, it does not deal with the order of events in the nervous system which are responsible for the alteration in the type of movement of a segment.

There are three characteristics of behavior mechanisms which must be taken into account if a comprehensive classification of this type is to be made. These are: (1) the relative extent of the stimulusogenous zone; (2) the number of different types of sense-organs whose stimulation will release essentially the same pattern of response; (3) the relative degree of segmental involvement or participation in a response.

Without touching upon the details of the scheme for representing quantitative degrees of specificity the possibilities of such a classificatory system may be made apparent by analyzing a few responses. Let us consider characteristic (3) in both the cross-sectional and the longitudinal views of the plantar response. Considered cross-sectionally, a response which

involves the toes, foot, leg and thigh is 'generalized,' *in the sense of segmental participation*, if compared with a response of the big toe alone, but is 'specific' in comparison with a response which involves contralateral as well as homolateral activity of the inferior extremities. Again, this latter response would be 'specific' in comparison with Moro's reflex. In the longitudinal plane at first there is greatest 'generalization,' followed by the progressive restriction of segmental participation, so that when complete individuation arises there may be movement usually of the big toe alone. Under certain physiological or pathological conditions there occurs a reversion to the earlier and more generalized forms (38) of the response.

The orientation and sucking reflexes which comprise the food-getting response afford an excellent illustration of characteristic (1). At birth, the reflexogenous zone extends over the lip and cheek areas, although even at that time a differential sensitivity may be demonstrated. With increasing age the frequency of response to cheek stimulation decreases—i.e., the reflexogenous zone becomes restricted (39). On the early neonate level the reflexogenous zone of the plantar response is more extensive or generalized, that of the palpebral (contact-aroused) more limited or specific, than that of the orientation and sucking reflexes.

Characteristic (2) (the number of different types of sense-organs the stimulation of which evokes the same pattern of response) is exemplified in the most generalized sense, in that stimulation of practically all kinds results in respiratory and circulatory changes; and this is also apparent in the release of the Moro reflex through auditory, visual, static and probably through other forms of stimuli. On the other hand, the area whose stimula-

tion will start the hiccup response (32) is well restricted to one bodily region.

Again, considered upon the cross-sectional plane, in the case of the Moro response we find the greatest involvement of the organism in the response to the first of a series of auditory stimuli, followed by a decrease in segmental participation in the responses to the further stimuli of the series (34). This phenomenon is typical of inhibitory mechanisms.

Finally, in the process of learning, such as in mastering the art of writing, Steinmann (45), and Gottstein and Gottstein-Schenck (19) find that initially generalized associated movements (*Mitbewegungen*) are the rule, and that the younger the child the more pronounced the intensity and the spread of the associated movements.

In the foregoing examples we have attempted to outline the principal features of a comprehensive classification of neonate behavior. The ordinary classification of responses, according to stimulus-receptor reference points, leads almost invariably to the impression of extreme multiplicity of responses, for almost every stimulus-receptor reference point gives rise to another name for the response despite the fact that in patterning of segmental participation it remains unchanged. A striking example of this is furnished by what is usually termed the plantar response. According to the cutaneous area stimulated we have 'Schaffer's reflex,' 'Gordon's paradoxical reflex,' 'Oppenheim's reflex,' etc., all of which refer to essentially the same response. Similarly, the pattern of movements which we have referred to as the Moro reflex (originally so-termed when the response is evoked by jarring the infant) has been called the 'primary emotion of fear,' the 'fear' response, the

'shock' response and the 'startle' reflex when elicited by auditory stimuli. Further, the throwing back of the head to various types of stimulation promises to develop a varied terminology according to the stimuli employed.

The comprehensive system of classification, on the other hand, presents a segmental analysis of a response and lists the types of stimuli and the sense-organs whose stimulation will bring it about. From this one tends to derive a picture of organismic activity rather than of highly fictionalized part activities. But its greatest advantage is in providing a quantitative expression of specificity, thus

making it possible to compare degrees of specificity at different levels in the genetic development of a response, or to effect such a comparison between different responses at the same age period. Further, it enables one to follow both the quantitative and qualitative changes contingent upon particular physiological states of the organism and upon those environmental influences which produce learning.

In conclusion, the principles of classification employed seem to have a truly genetic significance and are inclusive enough to furnish insight into both the cross-sectional and the longitudinal interrelations of human behavior.

## LIST OF LITERATURE

1. BABINSKI, J. Réflexes de défense. *Rev. Neurol.*, 1922, 38, 1049-1082.
2. BECHTEREW, W. M. Ueber die objektive Untersuchung der kindlichen Psyche. *Russki Wratsch.*, 1908, No. 16. (Abstract in *Folia neurol.*, 1908, 2, 362-366.)
3. BENEDICT, F. G., and TALBOT, F. B. The Gaseous Metabolism of Infants with Special Reference to Its Relation to Pulse-rate and Muscular Activity. Carnegie Instit. Wash., 1914, Publ. No. 201. Pp. 168.
4. BERSOT, H. Variabilité et corrélations organiques. Nouvelle étude du réflexe plantaire. *Schweiz. Arch. f. Neu. u. Psychiat.*, 1918, 4, 277-323; 1919, 5, 305-324.
5. —. Développement réactionnel et réflexe plantaire du bébé né avant terme à celui de deux ans. *Schweiz. Arch. f. Neu. u. Psychiat.*, 1920, 7, 212-239; 1921, 8, 47-74.
6. BLANTON, M. G. The behavior of the human infant during the first thirty days of life. *Psychol. Rev.*, 1917, 24, 456-483.
7. BUCK, F. From fundamental to accessory in the development of the nervous system and of movements. *Ped. Sem.*, 1898, 6, 5-64.
8. CANESTRINI, S. Ueber das Sinnesleben des Neugeborenen. (Monog. z. d. Gesamtgeb. d. Neu. u. Psychiat., No. 5.) Berlin: Springer, 1913, Pp. 104.
9. CARLSON, A. J., and GINNEBURG, H. Contributions to the physiology of the stomach. XXIV. The tonus and hunger contractions of the stomach of the new-born. *Amer. J. Physiol.*, 1915, 38, 29-32.
10. CARMICHAEL, L. Origin and prenatal growth of behavior. In Ch. 2 of A Handbook of Child Psychology, 2nd ed., rev., ed. by Carl Murchison, Clark University Press, 1933. Pp. 31-159.
11. CHILD, C. M. Physiological Foundations of Behavior. New York: Holt, 1924. Pp. xii + 330.
12. COGHILL, G. E. The early development of behavior in *Amblystoma* and in man. *Arch. Neu. & Psychiat.*, 1929, 21, 989-1009.
13. DARWIN, C. A biographical sketch of an infant *Mind*, 1877, 2, 285-294.
14. DENNIS, W. A description and classification of the responses of the newborn infant. *Psychol. Bull.*, 1934, 31, 5-22.
15. GEBELL, A. Maturation and infant behavior pattern. *Psychol. Rev.*, 1929, 36, 307-319.
16. GEBELL, A., and THOMPSON, H. Learning and growth in identical infant twins: an experimental study by the method of co-twin control. *Genet. Psychol. Monog.*, 1929, 6, 1-124.
17. GIVLER, R. C. The intellectual significance of the grasping reflex. *J. Phil.*, 1921, 18, 617-628.
18. GOODENOUGH, F. L. Developmental Psychology. D. Appleton-Century Co., 1934.
19. GOTTSHEIN, W., and GOTTSHEIN-SCHENCK, H. Koordination und Konzentration. *Zsch. f. Kinderforsch.*, 1933, 41, 1-44.
20. HURLOCK, E. B. Experimental studies of the newborn. *Child Development*, 1933, 4, 148-163.
21. IRWIN, O. C. The amount and nature of activities of newborn infants under constant external stimulating conditions during the first ten days of life. *Genet. Psychol. Monog.*, 1930, 8, 1-92.

22. IRWIN, O. C. The organismic hypothesis and differentiation of behavior: III. The differentiation of human behavior. *Psychol. Rev.*, 1932, 39, 387-393.
23. —. The distribution of the amount of motility in young infants between two nursing periods. *J. Comp. Psychol.*, 1932, 14, 429-445.
24. —. Proximodistal differentiation of limbs in young organisms. *Psychol. Rev.*, 1933, 40, 467-477.
25. LOWDEN, T. S. The first half year in an infant's life. *Past-grad. & Worcester Quar.*, 1895, Pp. 30.
26. MARQUIS, D. P. Can conditioned responses be established in the newborn infant? *J. Genet. Psychol.*, 1931, 39, 479-492.
27. —. A study of activity and postures in infants' sleep. *J. Genet. Psychol.*, 1933, 42, 51-69.
28. MINKOWSKI, M. Ueber frühzeitige Bewegungen, Reflexe und muskuläre Reaktionen beim menschlichen Foetus, und ihre Beziehungen zum foetalen Nerven- und Muskelsystem. *Schweiz. med. Woch.*, 1922, 52, 721-724, 751-753.
29. —. Neurobiologische Studien am menschlichen Foetus. *Abderhaldens Hdbh. d. biol. Arbeitsmeth.*, 1928, Abt. V, T. 5B, H. 5, 511-618.
30. MORGAN, T. H. The Physical Basis of Heredity. *Philadelphia and London*: J. B. Lippincott Co., 1919.
31. PREPER, A. Die Hirntätigkeit des Säuglings. *Berlin*: Springer, 1928. Pp. 102.
32. PRINDLETON, W. R. Hiccups among infants. *Amer. J. Dis. Child.*, 1927, 34, 207-210.
33. PRATT, K. C. The neonate. In *A Handbook of Child Psychology*, 2nd ed., rev., ed. by C. Murchison. *Worcester, Mass.*: Clark Univ. Press; *London*: Oxford Univ. Press, 1933. Pp. 163-208.
34. —. The effects of repeated auditory stimulation upon the general activity of newborn infants. *J. Genet. Psychol.*, 1934, 44, 96-116.
35. —. Specificity and generalization of behavior in new-born infants: a critique. *Psychol. Rev.*, 1934, 41, 265-284.
36. —. Generalization and specificity of the plantar response in newborn infants. The reflexogenous zone: I. Differential sensitivity and effector-segment participation according to the area of stimulation. *J. Genet. Psychol.*, 1934, 44, 265-300.
37. PRATT, K. C. II. Segmental patterning of responses. *J. Genet. Psychol.*, 1934, 45, 22-38.
38. —. III. The effects of the physiological state upon sensitivity, segmental participation and segmental patterning. *J. Genet. Psychol.*, 1934, 45, 371-389.
39. PRATT, K. C., NELSON, A. K., and SUN, K. H. The Behavior of the Newborn Infant. *Ohio State Univ. Stud.: Contrib. Psychol.*, 1930, No. 10. Pp. ix + 237.
40. PREYER, W. Die Seele des Kindes. *Leipzig: Fernau*, 1882. (5th ed., 1900. Pp. 462.) The Mind of the Child. Pt. I: The sense and the will. Pt. 2: The development of the intellect. (Trans. by H. W. Brown.) *New York*: Appleton, 1888, 1889. Pp. 346; 317. (Reprinted ed., 1901.)
41. RICHARDS, T. W., and IRWIN, O. C. Experimental methods used in studies on infant reactions since 1900. *Psychol. Bull.*, 1934, 31, 23-46.
42. SHERMAN, M., and SHERMAN, I. C. Sensorimotor responses in infants. *J. Comp. Psychol.*, 1925, 5, 53-68.
43. SHINN, M. W. Notes on the Development of a Child. *Univ. Calif. Publ.*, 1893-1899, 1, Pp. 424.
44. SHIRLEY, M. M. The sequential method for the study of maturing behavior patterns. *Psychol. Rev.*, 1931, 38, 507-528.
45. STEINMANN, I. Über Mitbewegungen bei Hilfschulkindern. *Zsch. f. Kinderforsch.*, 1931-32, 39, 83-115.
46. TALBOT, F. B. Physiology of the newborn infant. *Amer. J. Dis. Child.*, 1917, 13, 495-500.
47. TAYLOR, R. Hunger in the infant. *Amer. J. Dis. Child.*, 1917, 14, 233-257.
48. TIEDERMANN, D. Beobachtungen über die Entwicklung der Seelenfähigkeiten bei Kindern. (First published in 1787.) (Ed. by V. Ufer.) *Altenburg*: Bonde, 1897. Pp. vii + 56. Translation by C. Murchison & S. Langer. *J. Genet. Psychol.*, 1927, 34, 205-230.
49. WARREN, H. C. Human Psychology.
50. WATSON, J. B. Psychology from the Standpoint of a Behaviorist. *Philadelphia*: Lippincott, 1919, Pp. ix + 429.
51. —. Behaviorism. *New York*: Norton, 1925.

---



---

## NEW BIOLOGICAL BOOKS

*The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.*

### BRIEF NOTICES

#### EVOLUTION

HEAD, HEART AND HANDS IN HUMAN EVOLUTION.

By R. R. Marett. *Hutchinson's Scientific Books, London.* 10s. 6d. net. 8½ x 5½; 303; 1935.

The author, Reader in Social Anthropology at Oxford, is well known for his studies in anthropology and primitive religions. In this volume he discusses the three fundamental ways of organizing human experience—by means of the head, which provides categories or leading ideas; by means of the heart, which finds its chief expression in religion; and by means of the hands, which enable man, the manipulative animal, to abound in arts and crafts. The four sections of the book deal with the sociological outlook; pre-theological religion in general; pre-theological religion—particular illustrations; and primitive technology (arts and crafts of prehistoric and primitive man). Throughout the volume the writer argues for a better understanding of the underlying motives of customs and behavior. Acquaintance with different cultural connections helps the mind to detach essential values from their casual context and to measure them by the sole value of their intrinsic worth. Since on the economic plane we are gradually moving towards a relative uniformity of conditions and, even in its physical aspects, human life throughout the globe is threatened with a certain stupefying sameness, the writer

argues that the true work of man lies in "giving free scope to our natural variability on the side of the spirit." Tolerance of the playworld of the savage and of many of his customs which have always been quite healthy in their moral tone, will not let "his future be rendered as dark as that of many a drudge of civilization." Most of the material in this volume has either appeared in print or been given in the form of lectures. The work is indexed.



HEREDITY AND THE ASCENT OF MAN.

By C. C. Hurst. *The Macmillan Co., New York.* \$1.50. 7½ x 4½; ix + 138; 1935.

This is an admirably clear exposition for the general reader of genetics and its bearing on the problem of evolution. In Hurst's presentation the emphasized factors of evolution are mutation and hybridization rather than natural selection. Of particular interest is the account of the experimental creation of new species and recreation of known species.

These experiments demonstrate that gene mutations and transmutations may be either so minute as to be of slight taxonomic value, they may be small or varietal, or they may be large and specific, generic, tribal, or even familial and subordinal. . . . It is interesting to note that when a high group character like the two-celled ovary mutates it behaves like an ordinary varietal or Mendelian character. This fact, which has since been confirmed in generic and specific

characters in roses, shows that the higher taxonomic characters are determined by genes as well as the lower varietal characters.

In the last chapter the author leaves the solid ground of experiment and soars into the thin air of speculation. Since in the course of creative evolution mind has gradually increased in influence compared with matter, he extrapolates this trend to the conclusion that, with the help of a suitable eugenic program, "successors of Man may be evolved in whom the influence of matter has been almost, if not entirely, obliterated. In these conditions a less material or almost immaterial type of being might arise, utterly different from the present human species, scarcely human save in mind and intellect and on a higher intellectual plane. Such an independence of matter might enable the more adventurous spirits among our far-away descendants to leave the earth and to visit, and maybe occupy, other planets or stellar systems of our universe or even other universes if they exist."



#### THE CHANGING WORLD OF THE ICE AGE.

By Reginald A. Daly. Yale University Press, New Haven. \$5.00. 9½ x 6½; xix + 271; 1934.

A highly interesting book not only to students but to lay readers as well. The material was prepared originally for the Silliman lectures. Expanded in book form the author has included many tables, quantitative data, footnotes and references for advanced workers in this field, but the general reader will find little that is formidable. The latter part of the volume is devoted to the author's theory of the formation of coral reefs. He believes their origin was made possible by the Pleistocene changes of climate and the associated swings of sea level caused by the growth and melting of land ice. The arguments supporting this theory are discussed in great detail. The many excellent diagrams, charts and figures form a valuable part of the work. A detailed index is included.

#### GENETICS

Теоретические Основы Селекции Растений. Том I. Общая селекция растений.

Н. И. Вавилов, Главный редактор. Государственное издательство сельскохозяйственной литературы, Москва-Ленинград. 20 руб.; xx + 1043; 1935

[THEORETICAL BASIS OF PLANT BREEDING. Vol. I. General principles of plant breeding. Edited by N. I. Vavilov. State Publishing House for Agricultural Literature, Moscow-Leningrad. 20 roubles. 7 x 10 inches; xx + 1043; 1935 (cloth)].

This is the first volume of an excellently published and thoroughly documented monograph on plant breeding. It consists of a number of chapters written by different members of the Research Institute for Plant Breeding in Leningrad and edited by Professor Vavilov. Many of the results reported appear here for the first time, and a good use is made of Russian and foreign bibliography of the subject. As stated in the preface:

The first volume treats general problems and methods of selection as: geographic basis in selection, the principles of classification of economically important plants, the theory of mutations and of hybridization, the application of cytological, anatomical, biometric, biochemical and physiological methods in selection. Attention is paid to the methodology of selection for immunity against diseases and for cold and dry-hardiness. . . . All chapters have been reported and criticized before the Scientific Council of the Institute, and are here published in the form modified by discussion.

The volume consists of 5 parts including 29 papers written by 27 authors. Space does not permit us to mention all of them by name. As a matter of illustration we may take a paper by Professor Ivanov, "Biochemical basis of plant breeding." In his tables on variability in chemical composition of plants as related to race and environmental conditions he gives a great deal of hitherto unpublished data. For all plant breeders who read Russian this is a very valuable reference source.



#### GENETICS.

By H. S. Jennings. W. W. Norton and Co., New York. \$4.00. 8½ x 5½; xii + 373; 1935.

Dr. Jennings has written a clear and complete exposition of the fundamentals of genetics. This book, though intended for the layman, is far superior to the general run of science popularizers. The subject is presented in an orderly manner and at all times the reader is made aware of whether the author is discussing facts or theories. This is especially evident in the latter part of the book where the author examines the problems of heredity versus environment and of genetic variations. Characteristic is the concluding paragraph:

On the other hand it may turn out that gene mutations of the sort thus far observed are not the material of progressive evolution. It may be that we have not yet recognized the actual steps in progressive evolution, and that when these come clearly into view, it will be found that they are not the result of action of destructive agents, nor connected with injuries to the genetic system, but rather a resemblance to the changes of growth. These questions must be reserved for the future.

The bibliography is sufficient and in the reviewer's opinion this book could very well serve as a college text.



REPORT OF THE 11TH ASSEMBLY OF THE INTERNATIONAL FEDERATION OF EUGENIC ORGANIZATIONS. *Conferences July from 18th to 21st (inclusive) 1934, Waldbaus Dolder, Zurich, Switzerland.*

*Art. Institut Orrell Füssli, Zürich.* 10 Swiss francs; copies to members and correspondents of the International Federation of Eugenic Organizations at the office, 443 Fulham Road, London—3s. 6d. prepaid. 9½ x 6½; 84; 1935 (paper).

A report of papers read and discussed at the 11th Meeting of the International Federation of Eugenic Organizations. The introductory paper by Professor Rüdin, president of the Association, outlines the work of a German committee, aided by the Rockefeller Foundation, formed for the purpose of studying racial predisposition in Germany in relation to various mental diseases independent of asylum and clinical treatment. The second paper by Professor Berry of England deals with the diagnosis and grading of oligo-

phrenics. Dr. Mjöen of Norway discusses his methods for determining musical capacity. The fourth paper deals with personality and the present unsatisfactory state of the science. The fifth paper on racial psychology by Steggerda, deals with further attempts to measure personality. The fourth section of the conference was devoted to papers on twin work and the last part of the conference to a discussion by representatives from various countries concerning the status of eugenics in their respective countries.



DIE BLUTSVERWANDTSCHAFT im Volk und in der Familie. Ein Beitrag zur menschlichen Lebenskunde (Anthropologie).

By Walter Jankowsky. G. Schweizerbart'sche Verlagsbuchhandlung (Erwin Nägele), Stuttgart. 7.20 marks. 9½ x 6; viii + 166 + 6 plates; 1934 (paper).

The central problem of this book is that of resemblances in appearance, not only between members of a family but also between individuals who are not known to be related. In an effort to state and clear up this problem somewhat Jankowsky ably discusses the concepts of blood relationship, resemblance factors, the biological character and significance of the phenomena involved, individual heredity, pseudo-resemblances, and differences in members of the same family. He is cautious in formulating conclusions. A point of interest is the degree to which significance is to be attached to resemblances between unrelated persons on the theory of chance, and with special reference to conditions of descent within a given population.

This is a thought-provoking contribution, of interest to the ethnologist and student of human genetics. It contains a bibliography and is illustrated.



ANLEITUNG ZUR ERBIOLOGISCHEN BEURTEILUNG DER FINGER- UND HANDEKSTEN.

By Georg Geisfel. J. F. Lehmann, Munich. 5 marks (paper); 6.20 marks (cloth). 8½ x 6½; 80; 1935.



In this hand-book the author presents in turn a classification of finger prints and palmar friction skin patterns based on the Galton-Henry studies; a method of taking and classifying prints; and a discussion of the inheritance of patterns, based on his own work on 1500 pairs of twins, and that of Bonnevie. Several examples of establishing paternity by comparison of finger-prints are cited. The book is intended for the use of anthropologists, jurists, criminologists, biologists, and physicians. It is illustrated and has a short bibliography.



PHYSIOLOGIE DU DÉVELOPPEMENT ET GÉNÉTIQUE. *Actualités Scientifiques et Industrielles*, 254. *Exposés de Biologie (La Génétique et les Problèmes de l'Évolution)*, I.

By N. K. Koltzoff. Hermann et Cie, Paris. 12 francs. 10 x 6½; 56; 1935 (paper).

An interesting theoretical discussion of the processes of fertilization, cell division and early embryonic development, well written but distinctly speculative in character. This volume starts a new sub-series of the *Actualists*, under the general title *Exposés de Biologie*, to be edited by Professor Koltzoff. We shall await with keen interest further numbers.



#### GENERAL BIOLOGY

DIE MASCHINE UND DER ORGANISMUS.

By Hans Driesch. Johann Ambrosius Barth, Leipzig. 4.50 marks. 9½ x 6½; 76; 1935 (paper).

From certain points of view a living organism may be regarded as a machine. From the standpoint of kinetics both the steam engine and the horse are machines which transform chemical energy into mechanical energy. The question is whether all aspects of the activities characteristic of the living organism can be interpreted in mechanistic terms. If a fertilized ovum in its early stages of segmentation is cut in two, each half develops into a complete organism. Driesch in his previous writings has concluded that this process cannot be purely me-

chanistic, that a non-mechanical agent, an entelechy, must direct it. In the present book he extends his argument to behavior. This is not an invariable linkage of a certain detailed response to a certain stimulus; different responses, which attain the same end in different ways, may be called into action. If I lose my right hand I learn to write with my left. Here again Driesch concludes that a purely mechanistic interpretation is inadequate. Nerve conduction and muscle contraction may be purely mechanical processes, but there must be an entelechy to initiate the impulse over one nerve rather than another. An appendix contains Driesch's reply to the criticisms of Schlick and Carnap.



АНАБИОЗ.

П.Ю.Шмидт. Государственное издательство биологической и медицинской литературы, Москва-Ленинград. 5 руб. 65 коп.; 296; 1935.

[ANABIOSIS.

By P. J. Schmidt. State Publishing House for Biological and Medical Literature, Moscow-Leningrad. 5.65 roubles. 5 x 8 inches; 296; 1935 (cloth)].

The essential structure of living matter and the principles of operation of metabolic machinery are at present very imperfectly understood. Such attacks as Needham's valuable writings on the dissociability of the fundamental processes in ontogenesis are few in number, and the whole field lies open for intensive theoretical and experimental research. The attempts to stop life for a while tried in the "anabiotic" experiments can undoubtedly throw some light on metabolic machinery, and in this book a fascinating account is given of such attempts.

The book consists of Prolegomena, Epilegomena, and four chapters: (1) Latent life, (2) Anabiosis under desiccation, (3) The action of high and low temperatures on life processes, and (4) Anabiosis under freezing. Concerning the very possibility of the complete cessation of life processes the present author concludes:

All the reviewed experiments on the simultaneous action of low temperatures and more or less complete desiccation, and especially under complete exclusion of the oxygen of the air, show definitely that in some moss-inhabiting animals a reversible cessation of life has been actually observed. In these experiments any traces of metabolic processes are absolutely impossible, as no chemical reaction could go on at a temperature only a few degrees above the absolute zero, and gases participating in respiration are in the solid state.

There are perhaps some specific adaptations in these moss-inhabiting animals, and in many other cases, as Kalabuchov has recently shown, no such complete cessation could be experimentally realized. Schmidt therefore concludes:

We are at present only at the very beginning of the scientific study of anabiosis, which appears to be much more complicated than originally supposed. The main trails for research are already more or less clear, but a great deal of work and energy should be spent until the whole phenomenon will be mastered and used for our own ends.

This is a valuable review, and so far as is known no such book is available in any of the leading European languages. Anabiosis does not yet attract the attention which it undoubtedly deserves.



#### BIOLOGICAL PROCESSES IN TROPICAL SOILS *With Special Reference to Malaysia.*

By A. Steven Corbet. W. Haffer and Sons, Cambridge. 7s. 6d. net.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; xiv + 156; 1935.

The great diversity of climatic conditions throughout the tropics produces a wide variety of problems, but throughout the hot, wet equatorial belt conditions are so similar that there is much in this volume that is applicable to regions outside of Malaysia. Due allowance must be made, however, for variations in flora and fauna. The author, chemist and biologist at the Rubber Research Institute of Malaya, has written primarily for agricultural chemists, but planters and foresters in tropical countries will find the volume highly useful. Mr. Corbet states that the whole process of formation and decomposition of soil organic matter in the humid tropics seems to be based on

(a) Jenny's law that the "nitrogen and organic matter content of the soil varies inversely with the soil temperature and the amount of solar radiation received," and (b) "At temperatures below  $25^{\circ}\text{C}$ . there is an accumulation of organic matter in the soil but, at temperatures above this, humus decomposition outpaces its formation." These laws he discusses at considerable length. In the first chapter such questions are considered as the burning of cleared land, leguminous cover plants, natural covers, the effect of fertilizers on the soil, and garden soils. The volume is fully documented and in an appendix contains sections on (I) Standard methods employed for the examination of soils, and (II) Classification of bacteria. There are also illustrations, figures, charts and graphs, and author, subject and plant indexes.



#### PROBLEMS IN SOIL MICROBIOLOGY.

By D. Ward Cutler and Lettice M. Crump. Longmans, Green and Co., New York. \$3.20.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; vii + 104; 1935.

The purpose of this book is to show

... that from the biologist's viewpoint the soil is an eminently suitable home for living organisms and that, through the long ages of evolution, a population has been selected which is, on the whole, so unspecialized that almost any substance which finds its way into the soil, either naturally or in the course of modern agricultural practice, will eventually become incorporated into the general soil economy.

The book contains chapters on the following topics: the suitability of the soil for micro-organisms; the bacterial population of the soil under field conditions; the relation of the soil bacteria to nitrite; carbon dioxide production by soil; the growth of protozoa in pure culture; the behavior of protozoa in soil, and the interactions between the soil organisms. There is an index and a bibliography.

A significant piece of work which should prove interesting and stimulating to the general ecologist. Any careful investigation, such as this one, on the structure and analysis of a biotic community is a welcome addition to biological literature.

**ALTERS-FORSCHUNG.** *Untersuchungen und Berichte über Lebensdauer, Altern und Tod.* 1. Jahrgang.

Edited by Josef Kluger. Josef Kluger, Gartenstrasse 135, Wünschelburg-Hauschauer. 3 marks.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; 40; 1935 (paper).

The first volume of a periodical devoted to a resumé of recent thought and study of longevity. There are six different articles all apparently written by the editor who is at the same time sole contributor to Volume one. The first article is about some of the more obvious phenomena of old age, following which is a chart of the various branches of science which contribute directly or indirectly to our knowledge about age. A few pages are devoted to two articles: (1) Chief characteristics of age as seen on the skin; and (2) Hardening of the arteries as evidenced in old age. The editor then lightens the tone of the magazine by inserting a few quotations from famous people who have lived to an old age and reflected some upon it. The last two articles are about grey hair and long life among animals other than man. The magazine winds up with seven life histories, each a few lines long, five of whom are Germans 80 or over now enjoying good health, (6) an old hen aged 21 years, and (7) a rose bush blooming healthily since 1788. There is a brief reference to new publications on longevity.



#### THE TEACHING OF BIOLOGY.

By Mary E. Phillips and Lucy E. Cox. University of London Press, London. 4s. 6d. net.  $7\frac{1}{2} \times 4\frac{1}{2}$ ; viii + 155 + 4 plates; 1935.

This little volume is written by two women who have had experience in the teaching of biology to children, with the object of presenting to other teachers methods they have found most effective in creating a wide awake interest in biology and nature. The book is divided into three sections of about equal length. The first, entitled "The general principles that underlie biological teaching," is punctuated with quotations on child psy-

chology from various authors and gives simple answers to the questions of what are the aesthetic, ethical, logical and practical values of biology. Sections 2 and 3 have to do with general and special methods of directing and teaching biological work among children in age groups varying from the "under fives" to the sixteen year olds. Stress is laid on the great importance of observation and experiment and the recording of results in the form of notes, drawings and collections. Numerous methods and projects for arousing and maintaining a vital interest in the subject are briefly described and should be of real value to teachers of biology in the grades. There is an adequate index.



#### PROCEEDINGS AND TRANSACTIONS OF THE LIVERPOOL BIOLOGICAL SOCIETY, Volume 48. Sessions 1933-1934; 1934-1935.

Edited by R. J. Daniel, with the co-operation of S. T. Burfield and W. S. Laverock. University Press, Liverpool. 1 Guinea.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; xii + 97; 1935.

The most interesting paper in this report is that on the "Growth of the Young Lobster," by W. C. Smith.

The rearing experiments furnish evidence that moulting and mortality, in the case of young lobsters, are almost confined to the summer months, with temperatures over 10°C., and that the growth and death rates reach a maximum with temperature. They also indicate that June-hatched lobsters usually moult seven times in the first growth period, June-December, although some individuals may go through the process four, and others as many as eight times. Moulting occurs from two to five times in the second year, but principally three times; and the third year records show two or three moults, with one case of a single moult. There are four instances of fourth year lobsters, and they all moulted twice. One lobster moulted once, and another on two occasions, in the fifth year; and all later years up to eleven (for which there are records of one lobster) give one moult annually.

Tables of measurements at various periods are given.

A second article by the same author in collaboration with T. N. Cregeen tells of experiments to determine the optimum environment for rearing lobster larvae to the lobstering stage.

Колебания Численности Промысловых Животных.

А.Н.Формосов. Всесоюзное Кооперативное Об'единенное Издательство, Москва-Ленинград. 2 руб.; 108; 1935.

[FLUCTUATIONS IN NUMBERS OF GAME ANIMALS.

By A. N. Formosov. All-Union Co-operative Publishing House, Moscow-Leningrad. 2 roubles. 6 x 8½ inches; 108; 1935 (paper)].

In these days of the work of *The International Conference on Biological Cycles and Bureau of Animal Population* a book summarizing the data on periodic fluctuations in numbers of economically important Russian game animals comes as a welcome contribution.

Dr. Formosov, who is well known by his original investigations on the subject, has divided his book into two unequal parts. The first part dealing with mammals (pp. 3-86) gives an account of hare, squirrel, polar fox and common fox populations; the second part (pp. 87-106) treats hazel grouse, ptarmigan and some other birds. In conclusion he notes that fluctuations in numbers are more sharply outlined in animals possessing high fertility, and that the whole subject is of very great economic importance.



TISSUE CULTURE. *The Growth and Differentiation of Normal Tissues in Artificial Media.*

By E. N. Willmer. Methuen and Co., London. 4 shillings net. 6½ x 4½; xvi + 126 + 3 plates; 1935.

This little volume (of Methuen's Monographs on Biological Subjects) gives briefly but simply an account of the part played by the method of tissue culture, . . . , in helping to elucidate some of the problems of normal growth and differentiation, and in furthering the knowledge of the processes involved in the normal development of the animal organism." Obviously it has been impossible to give a full account of all the ways in which the method of tissue culture has been applied. The author has not touched on the subject of the growth of malignant cells, of the sensitivity of these and normal cells to radium and

x-rays, or of any of the applications of the method to problems of pathology. The volume is illustrated and well documented and contains an index.



PHÉNOMÈNES D'INTÉGRATION DANS LES CULTURES DES TISSUS. *Actualités Scientifiques et Industrielles* 240. *Exposés de Biologie (Embryologie et Histogénèse) IV.*

By Boris Ephrussi. Hermann et Cie, Paris. 8 francs. 10 x 6½; 24; 1935 (paper).

A short resumé of the investigations of the author and others on the growth, limit of size and form of tissue cultures. Among the conclusions drawn are: (a) Tissue cultures possess a tendency toward definite size and form. (b) The equilibrium of a culture as regards its growth and spreading out depends upon the media and optimum density of population, nourishment and waste products. (c) Cellular division and mitosis take place at the periphery, and the cellular elements become a heterogeneous rather than a homogeneous whole as the older cells change. (d) Cells seem to grow faster when they come from a large area and mass, and this accounts for the fact that healing takes place more rapidly in an invagination.



PROBLEMS IN EXPERIMENTAL EMBRYOLOGY being the *Thirty-sixth Robert Boyle Lecture*. *Delivered before the Oxford University Junior Scientific Club on May 26, 1934.*

By Julian S. Huxley. Oxford University Press, New York. 35 cents. 8½ x 5½; 17; 1935 (paper).

A popular exposition of some aspects of recent advances in experimental embryology. The address ends on the following note:

Experimental embryology differs from classical physiology in being concerned, obviously and all the time, with change, orderly but progressive. No transformations so radical nor so irreversible as these of embryology occur in the adult vertebrate body. It will be in developmental physiology that the concept of rate of biological change will first require thorough-going analysis. It is probable that, once analysed there, it will extend in fruitful influence through other branches of biology.

## Рост Животных.

Сборник работ под редакцией И. Шмальгаузена, В. Токина, С. Капланского и М. Мясникова. Государственное издательство биологической и медицинской литературы, Москва-Ленинград. 7 руб. 80 коп.; 368; 1935.

## [GROWTH OF ANIMALS.]

*Collected papers edited by J. Schmalhausen, B. Tokin, S. Kaplansky and M. Misykowsky. State Publishing House for Biological and Medical Literature, Moscow-Leningrad. 7.80 roubles. 6 x 9 inches; 368; 1935 (cloth).*

This book is written by Russian biologists who, during the last ten years, have contributed to the study of different aspects of the growth problem. Professor Schmalhausen has three papers: (1) Basic conceptions and methods of study of growth, (2) Growth and body size in their biological meaning, (3) Growth and differentiation. Doctor E. M. Wermel in a very thorough and readable review, "Size, multiplication and growth of cells," summarizes the results of his recent investigations on the subject. There are papers by Nasarenko and Spett, "On the hereditary factors of growth," and by Professor W. W. Alpatov on "Environment and animal growth."

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. Lieferung 444. Abt. V. Methoden zum Studium der Funktionen der einzelnen Organe des tierischen Organismus, Teil 10, Heft 5. Allgemeine und vergleichende Physiologie. Containing following articles: Einige Verfahren zur mikroskopischen Bestimmung der Brechzahlen von Zellen und Geweben, by W. J. Schmidt; Die Mikrostrahlstichmethode und andere Methoden des zytologischen Mikroexperimentes, and Transport von Sexualprodukten von Seeigeln in überlebendem Zustand für experimentelle Zwecke, by Sergei Tschachotin; Die Technik photographischer Aufnahmen bei mikroskopischen und fluoreszenz-mikroskopischen Lebendbeobachtungen, by Kurt Franke; Die wichtigsten mathematischen Methoden bei der Bearbeitung von Versuchsergebnissen und Beobachtungen, by Heinrich Reichel.

Urban und Schwarzenberg, Berlin. 14 marks. 10 x 7; 248; 1935 (paper).

Article I deals with several experiments on microscopical determination of refractive indices of cells and tissues. Article II concerns various microscopic rays to be used in cytological work. Article III deals with methods of transporting the sexual products of sea urchins in a living condition. Article IV is concerned chiefly with photographic technique of living material with the ordinary microscope and the fluorescent microscope. Article V is a discussion of biometric constants and formulas.



LES ASSOCIATIONS BIOLOGIQUES AU POINT DE VUE MATHÉMATIQUE. *Actualités Scientifiques et Industrielles*, 243. *Exposés de Biométrie et de Statistique Biologique*, V.

By Vito Volterra and Umberto d'Ancona. Hermann et Cie, Paris. 20 francs. 10 x 6½; 96; 1935 (paper).

In this book the authors develop mathematical equations which describe the interaction of animal and plant populations in various fundamental relationships. The following relations are considered: the variation in numbers of a single species living isolated in its environment; the relations of two species living together, and certain types of associations between many species. These three types of relationships are extended to a number of special cases such as predator and prey interactions, parasite and host interactions, competition between different species for food, etc. After formulating equations to describe these associations the authors conclude, by discussing the experimental work of themselves and others, that actual observations confirm many of the predictions made on mathematical grounds.

This monograph should be in the library of all students of quantitative biology. It is a scholarly contribution to this field.

## AN INTRODUCTION TO BIOLOGY.

By Edward L. Rice. Ginn and Co., Boston. \$3.20. 8¼ x 5½; xii + 602; 1935.

This volume is the outgrowth of the author's twenty-five years experience in teaching elementary biology in Ohio Wesleyan University. It is a sampling of the subject rather than a survey. After three introductory chapters in which are discussed: What is Biology?; Protoplasm, cells, tissues, organs, systems; and Osmosis, eight chapters are devoted to man and eight to the frog. Then follows a section on the classification of animals and five sections on the lower animals and plants. The last six sections are devoted to evolution, heredity and variation. In a series of appendices are given (a) Table of equivalents, (b) bibliography and (c) etymologies. The volume is well illustrated and indexed. An excellent text.



#### THE WORLD OF NATURE.

By H. C. Knapp-Fisher. Victor Gollancz, London. 6 shillings net.  $7\frac{1}{2} \times 4\frac{1}{8}$ ; 512; 1935.

This simply written little book makes the attempt to give some sort of indication of the characteristics of all the different sorts of living things in the world of nature. It is divided into four parts: The Sea Shore; An Outline of the Plant World; A Simple Survey of Insect Life; and Fish, Flesh and Fowl. Each chapter is so attractively introduced and the actual descriptions so delightfully and ingeniously written that it should fascinate the most unscientific of minds, young and old.



#### LOGIK UND SYSTEM DER LEBENSWISSENSCHAFTEN.

By Fritz M. Lehmann. Johann Ambrosius Barth, Leipzig. 7.30 marks.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; vii + 124; 1935 (paper).

A practicing physician believes that the scientific world needs a new theory of life processes, and herein gives a recipe. This new dish—a hashed assortment of transcendental dialectics, Faustian empirical philosophy, and the biology of healing processes and other aspects of medical and physical sciences—is labeled metabiology.

The author lists and discusses the ingredients but leaves the final mixing and cooking to other persons, presumably to be inspired by this book.



#### URDEUTSCHLAND. Deutschlands Naturschutzgebiete in Wort und Bild. Lieferungen 11, 12.

By Walther Schoenichen. J. Neumann, Neudamm. 2 marks each, or 24 marks for complete set; 28 marks bound volume. A cover for the complete volume may be purchased from the publisher for 2.50 marks.  $10\frac{3}{4} \times 8\frac{1}{2}$ ; Lief. 11, 241-272 + 8 plates; Lief. 12, 273-319 + xi + 9 plates; 1935 (paper).

These two numbers complete the first volume of an illustrated discussion of the geological formation, and the flora and fauna of Germany. Previous numbers have already been noticed in these columns (Vol. 10, numbers 3 and 4). Volume 1 is devoted to the geology.



#### STUDENT'S MANUAL IN BIOLOGY.

By Frederick L. Fitzpatrick and Ralph E. Horton. Houghton Mifflin Co., Boston. 48 cents.  $11 \times 8$ ; iv + 155; 1935 (paper).

This manual is designed as a student notebook, or guide in studying demonstrations in the laboratory. It is designed especially to be used with a textbook by the same authors, but could be profitably used with any good text.



#### HUMAN BIOLOGY

A DOCUMENTARY HISTORY OF PRIMITIVISM AND RELATED IDEAS. Volume I. *Primitivism and Related Ideas in Antiquity*.

By Arthur O. Lovejoy and George Boas, with Supplementary Essays by W. F. Albright and P.-E. Dumont. The Johns Hopkins Press, Baltimore. \$5.00.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; xv + 482; 1935.

This is the first volume in an ambitious and important scholarly undertaking. Its object is to set forth in detail and support

with extensive quotations from the original sources an idea, or better a group of ideas, that mankind has been prone to entertain from time to time since the beginning of his recorded history—namely the notion that the life of primeval men, or of men of some remotely earlier time, or of "savage" peoples, was a better life than that of civilized men. It is evident that this is a matter of great interest to all students of human biology. To them this volume and its successors as they appear will be a useful and valued reference source book, as well as to students of literature, history and philosophy to whom the work is more particularly addressed. This first volume deals with the thought of ancient Greece and Rome on the point, with brief supplementary essays on primitivism in ancient western Asia (Mesopotamia and Israel) and in ancient India.

The theme and counter-theme that run through the whole history of primitivism are:

1. "There were giants in them days."
2. "Frail men from grace did fall."

Precisely when, where and why the giants or the falling occurred is never specified in too great detail. But the general idea that they did is in Homer and Hesiod, just as it is in the latest bulletin of the last organization set up to save the nation.

The reputation of the authors is a sufficient guarantee of the soundness and thoroughness of the work. All quotations are first given in the original language, and followed by an English translation, the latter being done evidently with an eye rather more to precision than grace. We do not mean to imply that the translations are generally awkward in their literalness. Quite the contrary is the fact. But, as an example, while it is true that *δάκτυλον ἐκτείνειν* (p. 127) means precisely "to stretch out a finger" Eusebius's context leaves no doubt that the more idiomatic English rendering "lift a finger" would have done no damage to his thought.

We strongly recommend this book to our readers. In a quite literal sense no library worthy of the name will be without it.

#### MAN THE UNKNOWN.

By Alexis Carrel. *Harper and Bros.*, New York. \$3.50. 8½ x 5½; xv + 346; 1935.

This book was classified in a recent book-list under the head of Fiction. This was, no doubt, unintentional; yet one comes with a shock on such a passage as the following in the work of an austere experimentalist like Carrel.

Our present conception of the influence of prayer upon pathological lesions is based upon the observation of patients who have been cured almost instantaneously of various affections, such as peritonsillar tuberculosis, cold abscesses, osteitis, suppurating wounds, lupus, cancer, etc. The process of healing changes little from one individual to another. Often, an acute pain. Then a sudden sensation of being cured. In a few seconds, a few minutes, at the most a few hours, wounds are cicatrized, pathological symptoms disappear, appetite returns. Sometimes functional disorders vanish before the anatomical lesions are repaired. The skeletal deformations of Pott's disease, the cancerous glands, may still persist two or three days after the healing of the main lesions. The miracle is chiefly characterized by an extreme acceleration of the processes of organic repair. There is no doubt that the rate of cicatrization of the anatomical defects is much greater than the normal one. The only condition indispensable to the occurrence of the phenomenon is prayer. But there is no need for the patient himself to pray, or even to have any religious faith. It is sufficient that some one around him be in a state of prayer. Such facts are of profound significance. They show the reality of certain relations, of still unknown nature, between psychological and organic processes. They prove the objective importance of the spiritual activities, which hygienists, physicians, educators, and sociologists have almost always neglected to study. They open to man a new world.

We wish that the author had had space to present the records on which these statements are based. We are prepared to admit that there may be more things in the relation of mental to physiological processes than are dreamt of in the current orthodoxy of science but the correction of the skeletal deformations of Pott's disease in a few days taxes our belief.

As a whole the book develops a program for the synthesis of physiology, psychology and the social sciences into a science of man. Carrel is no admirer of present-day civilization in many of its aspects. The lagging of our knowledge of man behind that of the external world, the too sheltered environment and the consequent disuse of the adaptive functions, are fraught with danger. Yet



there is a beacon of hope in the darkness. "Medicine aggrandized according to the conception of Descartes, and extended in such a manner as to embrace the other sciences of man, could supply modern society with engineers understanding the mechanisms of the body and the soul of the individual, and of his relations with the cosmic and social world."

The proposal is an arresting one. These superphysicians, these social engineers, might not solve all the problems of humanity; yet we have a suspicion that they might well do a better job than the present masters of mankind.



#### LE DESTIN DES RACES BLANCHES.

By *Henri Ducugis*. *Librairie de France*, Paris. 38 francs. 10 x 6½; vii + 402; 1935 (paper).

In common with most people, the author is appalled by the present economic conditions, but unlike many economists he is unable to perceive any benefits to be derived from governmental interference in business. The author's method of analysis of economic trends is simple and straightforward. He presents a summary of statistical information regarding the changes in production cost and distribution of the more important commodities, the developments in transportation, international finances, etc. He also discusses population questions and political forms of government. He believes that in the United States the liberal form of government is rapidly coming to an end. The conclusions reached are not novel, but in the form stated by the author appear excessively pessimistic. They may be summarized as follows: (1) Europe has lost its economic and financial hegemony, its tariff barriers serve only to prolong the agony of a dying agriculture and industry; (2) the industry of the United States is geared to a production higher than its marketing possibilities which government aid to farmers cannot possibly augment; (3) Japan has successfully invaded the world's market with its products and in China has not only a large unexploited market but also a rich source of raw materials. The author does

not attempt to find a remedy for these conditions but emphasizes that a continuation of the post-war government policies will only make matters worse. It is evident that this book presents nothing new, but it is superior to some similar recent studies because (a) it is factual (in minor instances the sources of data do not appear reliable) and, (b) there is an attempt, very feeble indeed but still an attempt, to view our present civilization as only one phase in the general evolution of man. The increasing number of unemployed, the excessive government interference in commerce, the decrease in birth-rates, etc., were observed and associated with the decline of ancient Greece and Rome. The author fears that at present they are symptoms of the decline of European civilization.



#### THE MEDICAL MAN AND THE WITCH DURING THE RENAISSANCE. *The Hideyo Noguchi Lectures*.

By *Gregory Zilboorg*. *The Johns Hopkins Press, Baltimore*. \$2.50. 7½ x 5½; x + 215 + 4 plates; 1935.

Probably the earliest view of disease, both mental and physical, was that it is the result of possession by an evil spirit or of the maleficent spells of a sorcerer. Although the Greek physicians from Hippocrates to Galen regarded both types of disease from a naturalistic viewpoint, their successors washed their hands of psychiatry, leaving the problem to the theologians and lawyers, who, as usual, made an inhuman mess of it. The real founder of modern psychiatry was Johann Weyer, whose *De Praestigiis Daemonum* was published at Basel in 1563. In this he ridiculed the tales of witches riding through the air to their sabbaths and insisted that the proper person to treat mental ills was not the exorcist but the physician. He attributed many of the supposed effects of sorcery to poisons and the delusions of those accused of witchcraft to such drugs as belladonna and opium.

It was not until a later age that Weyer's attitude towards psychopathology was generally adopted. The reaction of his



contemporaries is typified by the contemptuous dismissal of his arguments in the Saxon criminal code of 1572. "since he was a medical man and not a jurist." His own church placed his writings on the *Index Librorum Prohibitorum* where they remain to this day. Does this mean that a Roman Catholic psychiatrist is bound by his faith to turn over his patients to the ecclesiastical courts for trial as witches?



CIVILISATION AND THE GROWTH OF LAW.  
*A Study of the Relations Between Men's Ideas About the Universe and the Institutions of Law and Government.*

By William A. Robson. The Macmillan Co., New York. \$2.50. 8½ x 5½; xv + 354; 1935.

The author outlines the gradual evolution of law, and notes the progress from the primitive assumption that directly or indirectly it was derived from supernatural powers to the modern concept that it is a product of society. He shows how at different periods law has been influenced by superstition, religion, philosophy and science. Science itself has passed through a similar evolution. He observes that until recently "the wheels of the universe were supposed to revolve in a purely objective and mechanical way and it was felt to be a grave impropriety to suggest that the laws which described their movements had any relation to human life or thought" (p. 328). But now, . . . "it is the human mind which both formulates the pattern of physical conduct we call natural law and also establishes the pattern of social conduct we call human law" (p. 328). So, he concludes that since man now realizes that he is free to create whatever type of society he desires (and also whatever solar system he wishes, one can presume) probably he will do so and much misery and unnecessary suffering will eventually pass away.

We admire the brilliant style in which the book is written and the erudition of the author; and enjoy the formal logic employed in the discussion but regard such a conclusion as something of an anticlimax. Since time immemorial, no

matter what their superstitions or religious beliefs, men have tried to find some way to overcome social misery and suffering, but unfortunately, they have never agreed, either on the method or on a satisfactory definition of the objective.



THE INDIAN PEASANT AND HIS ENVIRONMENT.

(*The Linlithgow Commission and After*).

By N. Gangulee. Oxford University Press, New York. \$4.00. 8½ x 5½; xxiii + 220 + 8 plates; 1935.

By means of selected letters written to various persons during the many years he has been studying Indian agriculture and rural problems, and extracts from his journal kept during 1926-28 while serving as a member of the Royal Commission on Indian Agriculture (of which Lord Linlithgow was chairman) Prof. Gangulee pictures the agricultural problems and agrarian discontent as they exist in India. The letters and extracts are classified into five chapters. The first, "Glimpses into Indian Villages," sets forth the fundamental handicaps under which the Indian peasant (ryot) labors: Illiteracy, disease, complicated land tenure systems, pernicious money lending schemes, absence of suitable subsidiary occupations, lack of irrigation facilities, inadequacy of agricultural machinery and methods, etc. Chapter II, "Economic Life in Rural India," shows the necessity of reconstructing the entire organization of the cultivator, the necessity of a thorough overhauling of Indian land tenure systems to bring them into conformity with the needs of modern agriculture, coöperative movements to extricate the peasant from the clutches of the money lenders, and to provide him with adequate resources to enable him to avail himself of improved techniques for raising and marketing agricultural products.

In Chapter III, "Social Life, Education and Health in Rural India," Dr. Gangulee pleads for education of the masses to stamp out illiteracy, "the root cause of all our troubles"; malaria, "our most indigenous enemy" and malnutrition, "perhaps our chief disability"; and paves

the way for a program of "Rural Reconstruction in India" (Chapter IV), the first objective of which must be "directed to the means by which he [the peasant or cultivator] may be made conscious of his legitimate rights so that he himself may know what to demand and how to demand it." The last chapter, "The Government of the Masses," is made up of several letters on the constitutional problems of rural India, recommending that the constitution makers become better acquainted with the conditions of the peasantry and the constitution under the reforms be raised on the foundation of local self-government.

The book is well illustrated with photographs; there is a glossary of Indian words, and an index. An interesting and valuable contribution.



#### PRIMITIVES AND THE SUPERNATURAL.

By Lucien Lévy-Bruhl. *Authorized Translation by Lilian A. Clare.* E. P. Dutton and Co., New York. \$5.00. 8½ x 5½; 405; 1935.

In this interesting book the author treats in more detail than in his previous works certain aspects of the attitude of primitive peoples towards the supernatural influences which to their way of thinking are the real masters of their destiny. Surrounded by a hostile and incalculable environment, to which their predominant reaction is fear, they see no hope of safety except in "a pious adherence to the protective traditions handed down by former generations. In spite of the dangers menacing them on all hands their ancestors were able to live and to transmit life. With that life their descendants received from them a code of precepts and prohibitions, the faithful observance of which will enable them to survive like their fathers, and to secure the perpetuity of the group."

Among the subjects treated are good and bad luck, the favorable or unfavorable "dispositions" of the unseen powers, the ritual ceremonies and dances by which they are propitiated, the worship of ancestors and of the dead, witchcraft, incest,

defilement and purification, the magic virtues and sinister powers of blood, and methods of purification.

Our own feeling towards this, as towards Lévy-Bruhl's other works, is that he is inclined to overemphasize the gap between the mind of primitive and of modern man, to neglect the survivals of pre-logical mentality among more highly developed cultures. For instance, he mentions the belief in bi-presence as characteristic of primitive modes of thought; yet to the men of the Middle Ages the bi-presence of St. Anthony of Padua was matter of common belief.



#### ESSAYS OF WILLIAM GRAHAM SUMNER. *In two volumes.*

*Edited, with Prefaces, by Albert G. Keller and Maurice R. Davis.* Yale University Press, New Haven. \$3.00 per volume. 8½ x 6; Vol. 1, xix + 409; Vol. 2, viii + 534; 1934.

Professors Keller and Davis and the Yale University Press have done the world a signal service in producing this definitive edition of Sumner's essays. William Graham Sumner was not only by a long way the greatest sociologist America has produced; the science itself has had but very few men in its history of Sumner's intellectual caliber. He was that rare sort of person who could be a thorough scholar and not at the same time be a pedant. Nearly everything he ever wrote could be read with both pleasure and understanding by any intelligent man. Furthermore much of it was published in places easily accessible to the non-academic public. It is reasonable to suppose that these attributes of his work were not accidents. Instead he saw, as Huxley did, that scholarly effort that deliberately confines itself to the narrow circle of professional colleagues not only is practising self-mutilation, but is making more difficult the whole task of the advancement of learning. For if science is to live it can only be through the good will and support of the public in the long run.

Seldom has Sumner's moral courage been matched in the history of mankind.

He blasted quackery wherever he saw it, regardless of potential consequences, personal or institutional. The longest essay of the lot exposes, and then annihilates with a consuming fire of logic and ridicule that Sacred Cow of 100-percent Americanism, the theory of protective tariffs.

We predict that these beautifully produced and soundly edited volumes will have a large and steady sale. They embody a contribution to human thought of permanently enduring value.



MIGRATION AND PLANES OF LIVING, 1920-1934.

By Carter Goodrich, Bushrod W. Allin and Marion Hayes. *University of Pennsylvania Press, Philadelphia*. \$1.00. 10 x 6 $\frac{1}{2}$ ; viii + 111 + 2 folding maps; 1935 (paper).

This survey has for its purpose to build up a part of the factual basis on which an intelligent migration policy might be predicated. The first survey by C. Warren Thornthwaite published in 1934 was concerned with an analysis and mapping of past currents of internal migration, beginning at the earliest time at which they could be studied in the state-of-birth figures of the Census and continuing in greater detail with the somewhat more abundant data of recent decades.

The present bulletin presents estimates of population changes over a considerable portion of the country for the years since 1930 and discusses the question of whether "those who moved gained or lost, and to what extent have their migrations performed the function, so eloquently described in the simpler textbooks of economics, of moving labor from points of redundancy to points of need?" Throughout the text will be found the data arranged in tables and graphs and charted on maps. Appendix A explains the mapping of special types of areas, Appendix B gives the tabular analysis of special types of areas grouped according to percentage of population on relief, and Appendix C discusses the reliability of school census data.

WHITE MAN'S COUNTRY. *Lord Delamere and the Making of Kenya*. Volume I, 1870-1914; Volume II, 1914-1931.

By Elspeth Huxley. *The Macmillan Co., New York*. \$10.00 for the two volumes. 8 $\frac{3}{4}$  x 5 $\frac{1}{2}$ ; Vol. I, xiii + 315 + 12 plates and 2 folding maps; Vol. II, vii + 333 + 12 plates and 2 folding maps; 1935.

This thorough and scholarly treatise is essentially a biography of Hugh Cholmondeley, third Baron Delamere, set in the background of the history of Kenya Colony. Delamere believed that Kenya was a "white man's country" from the day he first hunted over it as a young man. He devoted his life and his fortune to proving his point and making other people believe it too. England ran the country from the Colonial Office in London in the best British tradition of stupid muddle-headedness. Delamere derived great pleasure and satisfaction from periodically telling the Pooh-Bahs back home and in Nairobi precisely what he thought of them. On the evidence his command of picturesque profanity must have been nearly or quite unparalleled in recent times. He further enjoyed the enormous advantage of being able, when things got too thick, to go home and take his proper seat in the House of Lords and from that vantage point tell Government where to alight. Altogether he was a wicked fellow, but a grand man. He devoted his life unselfishly and unstintingly to making a fine and high ideal a reality.

The book is a superb piece of historical research and writing. It will long stand as a reference work of first importance to students of colonization, ethnology, and sociology generally.



NASKAPI. *The Savage Hunters of the Labrador Peninsula*.

By Frank G. Speck. *University of Oklahoma Press, Norman*. \$3.50. 9 x 6; 248 + 20 plates; 1935.

Professor Speck sets forth in this book the first study of the religious life of the Montagnais-Naskapi, seminomadic bands

living in perhaps the most physically exacting and rigorous climatic environment of any peoples of the earth. Essentially a race of hunters, obtaining subsistence solely by the chase, these crude and simple people "have worked out a spiritualistic system as complete and as artificial for gaining control over animal spirits as their hunting devices and weapons are effective in accomplishing the physical slaughter of game" and remain impervious to any teaching which does not satisfy their emotional needs. Hunting is to them a holy occupation and since through animal life health and happiness come to the Naskapi, animals become the primary objects of religious zeal. This is manifest in their art, their dancing, and their games.

Special chapters are devoted to spiritual forces, concept of the soul, concepts of mythology and the universe, animals in special relation to man, divination, magic practices, medicinal practices and charms for hunting. A glossary of Indian words, an explanation of characters employed in recording native terms and an index complete this interesting and thought-provoking book.

This study is the tenth volume in the "Civilization of the American Indian Series," published by the University of Oklahoma Press.



**THE TARAHUMARA.** *An Indian Tribe of Northern Mexico.*

By Wendell C. Bennett and Robert M. Zingg. University of Chicago Press, Chicago. \$4.00. 8½ x 5½; xix + 412 + folding table; 1935.

This ethnological study is concerned with one of the largest tribes of American Indians north of Mexico City. The authors took up their abode with these Indians and studied all aspects of their culture. They have produced an authentic and highly interesting book. Living in the isolated mountain regions of the Sierra Madre in the summer and migrating in the colder months to the warmer caves of the rivers, the Tarahumara have maintained to a marked degree their simple

aboriginal culture. The thin veneer of Spanish culture is recognizable with considerable certainty. Violins and guitars are manufactured with a fair amount of skill. The native fiestas are of ancient origin and involve only the Tarahumara daily life. The church fiestas, introduced by a priest 40 or 50 years ago, have been absorbed but greatly modified and extended by native imagination until today they form one of the most important parts of the social culture of the Indians.

The volume contains a number of plates and diagrams, a bibliography and an index. Of particular value to the student is the excellent tabular analysis of the culture of Sonoran Uto-Aztecan tribes.



**ANTHROPOLOGY IN ACTION.** *An Experiment in the Iringa District of the Iringa Province, Tanganyika Territory.*

By G. Gordon Brown and A. McD. Bruce Hutt. Oxford University Press, New York. \$2.75. 7½ x 4½; xviii + 272 + folding map; 1935.

This book is the outcome of an interesting experiment made possible by a grant from the Rockefeller Foundation. Its object was to determine whether, and in precisely what ways, a thorough anthropological study of a native group by a trained specialist, would be practically useful in the administration of the group. The group on which the experiment was tried was the Hehe tribe living in the Iringa district of Tanganyika Territory. Brown was the anthropologist and Hutt the administrator. Both were experienced in the district before the specific undertaking started. The general result as set forth in the book is a sound, well reasoned, and judicious, if not particularly exciting contribution. One gets the impression that the Hehes will, on the whole, profit more from the writing of the book than anyone else, though few if any of them will probably ever read it. They are passing through a difficult cultural transition phase, and will undoubtedly be better administered as time goes on because this work has been done. The book has an adequate index.

TESTS AND MEASUREMENTS IN THE SOCIAL SCIENCES. *Report of the Commission on the Social Studies, Part IV.*

By Truman L. Kelley and A. C. Krey. Charles Scribner's Sons, New York. \$3.00.

7 $\frac{1}{2}$  x 5 $\frac{1}{8}$ ; xiv + 635; 1934.

The Commission on the Social Studies in the Schools started its work with high hopes of the applicability of new-type tests to the teaching of the social sciences. However, as the work progressed the social scientists on the Commission seem in general to have concluded that, while the new-type test is well adapted to measuring knowledge of specific events and of the simpler relationships of this material, "the more advanced and complex stages of these values . . . must as yet be discovered by other forms of test." The tests developed in the work of the Commission and described in this book relate to the understanding of the vocabulary of the social sciences, the ability to read maps, to draw other geographical inferences and to use historical evidence, and to the diagnosis of traits of character. There is a bibliography of 24 pages but no index.



LA COSTITUZIONE NELLE ARISTOCRAZIE ITALIANE. *Pubblicazioni della Università Cattolica del Sacro Cuore. Statistica, Vol. VIII.*

By Carlo Mengarelli. Università Cattolica del Sacro Cuore, Milano. L. 15. 10 x 6 $\frac{1}{2}$ ; viii + 165; 1935 (paper).

The author has compared the mean stature and weight of three samples of Italian men. These are: (a) university teachers and artists, (b) leading business men, members of parliament and high state functionaries, (c) life insurance policy holders. Keeping the average age and "racial" composition of the groups constant, it is found the men of category (b) are the tallest and the policy holders are the shortest. With stature also made constant, the group of university teachers and artists is inferior in weight to the other two groups.

This study is characterized by the painstaking efforts of the author to ascertain

that the three groups were really comparable to each other for the purpose of this investigation. There is an interesting discussion on the problem of the somatic constitution of the "élites," but it seems doubtful this type of study can contribute much towards a solution of this question.



INDIANER-RASSEN UND VERGANGENE KULTUREN. *Betrachtungen zur Volksentwicklung auf einer Forschungsreise durch Süd- und Mittelamerika.*

By Richard N. Wegner. Ferdinand Enke, Stuttgart. 15 marks (paper); 17.50 marks (cloth). 10 $\frac{1}{2}$  x 7 $\frac{1}{2}$ ; viii + 320 + 128 plates; 1934.

With the exception of the final chapter which treats of the Mayas of Yucatan, this book describes the culture, habits, games, appearance, and surroundings of some South American Indian tribes (almost exclusively those inhabiting the Chaco districts of Paraguay and Bolivia, and Peru) visited by the author in his travels during 1927-29. Historical matter is included concerning former cultures, migration, numbers, inter-racial and inter-tribal marriages, etc., as gleaned from records of early explorers. There is little new information concerning the Incas and Mayas. However, the study of the lesser known Chaco tribes is a contribution of value to ethnologists and geographers.

The book is adorned with 128 very fine photographic plates, including some excellent portraits, and distinctive pen and ink drawings serving as head- and tail-pieces for the 14 chapters. It is documented.



CULTURE AREAS OF NIGERIA. *Frederick H. Rawson-Field Museum Ethnological Expedition to West Africa, 1929-30. Field Museum of Natural History Publication 346.*

By Wilfrid D. Hambly. Field Museum of Natural History, Chicago. \$2.00. 9 $\frac{1}{2}$  x 6 $\frac{1}{2}$ ; 140 + 68 plates; 1935 (paper).

The first part of this report describes the types of industries found in Nigeria and the characteristics of their products.

North of 9° N. L. the culture is preponderantly of the Mohammedan type and shows clearly the effect of diffusion, by immigration and other contacts, from the north of Africa across the Sahara. This type of culture evidently replaced the indigenous, typically Negro, which is more and more prevalent as one proceeds south from the 9° parallel to the region of the dense tropical forests. The author indicates in convincing manner the interrelationship between geographical condition, history of migrations and the blending and differentiation of cultural patterns. The second part of this monograph includes brief comments on the customs of the several peoples inhabiting Nigeria. The clear verbal descriptions are rendered more interesting by numerous illustrations and photographs.



AGRICULTURE IN SOUTHERN AFRICA. *United States Department of Agriculture Technical Bulletin No. 466.*

By Clifford C. Taylor. U. S. Government Printing Office, Washington, D. C. 30 cents. 9½ x 5½; 342; 1935 (paper).

This bulletin presents a survey of the conditions and trends of agriculture in South Africa. The author analyses the quantity and quality of production, and the methods of marketing and exportation of the more important commodities such as wool, mohair, fruits, tobacco, cotton, sugar, cattle, and corn. From this analysis it appears that the production of wool, mohair and exportable corn is decreasing while that of cattle, citrous fruit, deciduous fruit and sugar is increasing. It is evident that a similar trend will eventually affect international trade and especially American exporters.

The facts here contained have been well assembled and brought to date. They also include data on the populations and on the physical characteristics of the different regions.



IS INDUSTRY DECENTRALIZING? *A Statistical Analysis of Locational Changes in Manufacturing Employment 1899-1933.*

By Daniel B. Creamer. *University of Pennsylvania Press, Philadelphia.* \$1.00. 10 x 6½; xii + 105; 1935 (paper).

The author presents statistics of the number of wage earners employed in all manufactures from 1899 to 1933 and in 24 industries from 1928 to 1933, distributed according to geographical regions and according to defined categories of industrial areas. He notes that in the principal cities the number of wage earners has decreased but that a decentralization of the major industrial centers has not been apparent until 1932-1933. The only real sign of decentralization is found in the South Atlantic states (not of great industrial importance) and for certain branches of the textile and of the boot and shoe industries. The author has apparently extracted all the possible information from the meagre data available and discusses the results in an objective manner.



OUTLOOK UPON THE FUTURE OF BRITISH UNEMPLOYED, MENTAL PATIENTS, AND OTHERS.

By Nathan Israeli. *Science Press Printing Co., Lancaster, Pa.* 50 cents. 10 x 7; 30; 1935 (paper).

By means of multiple choice questionnaires the author has sought to measure and compare "the outlook upon the future" of selected groups of British unemployed, mental patients, university students and superior high school students. The results seem to indicate that in certain particulars the unemployed are even less hopeful about their future than patients with anxiety neurosis. On the other hand the superior high school students are strikingly similar to the manics in manifesting a high degree of optimism. Although these results conform to expectations, there always remains the doubt if these tests, as well as others of the same type, actually achieve the intended objectives.



GOOD FOOD FROM SWEDEN. *Selections from Swedish Dishes Suited to an English Table.*

*Compiled by Inga Norberg. Chatto and Windus, London. 5 shillings net. 7½ x 5; vii + 176; 1935.*

The Swedes are husky eaters and drinkers, as any wanderer into the *Hinterland* of their charming country soon learns. Furthermore they have a long tradition of good cooking, about which the casual tourist who lives on the internationalised quasi-French cuisine of the first-class hotels in big cities knows nothing. This little volume does a real service in letting the world know that all Swedish food is not "outside works," as the conscientious doughboy in his innocence translated *bors d'oeuvres*. In reading it over, however, one is struck again by the fact that the national taste, as is proper in so northern a clime, runs strongly to food that will "stick to the ribs"—good solid stuff with a high calory yield per unit consumed.



**THE TRESSÉ IRON-AGE MEGALITHIC MONUMENT.** *Its Sculptured Breasts and Their Relation to the Mother-Goddess Cosmic Cult.*

*By V. C. C. Collum. Oxford University Press, New York. \$4.00. 10 x 7½; xiv + 170 + 35 plates; 1935.*

By a careful technique of excavation the author was enabled to prove that the Gallo-Roman pottery and iron sword which were found were not due to later disturbance and that therefore this megalithic tomb had been erected during the Roman occupation of Gaul. The four human breasts sculptured in relief are related by the author to the cult of the Great Mother, so popular in Armorican Gaul during the Roman occupation. She traces the cult in Egypt, Mesopotamia, India and Greece as well as its survivals in early Irish mythology. There is a bibliography of eight pages.



#### HASHISH.

*By Henry de Monfreid. Translated by Helen B. Bell. Methuen and Co., London. 10s. 6d. net. 8½ x 5½; vii + 284 + 9 plates; 1935.*

"Hashish" tells of the author's adventures

in smuggling this drug into Egypt. He buys it in Greece, ships it to Djibouti and then brings it up the Red Sea in a small boat. His adventures are vividly told and his enemies and accomplices well-drawn, but his frequent references to his earlier books are likely to be annoying and confusing to those who have not read them. For the discerning student of human biology there are many bits of useful material scattered through the book.



#### FOLK-LORE FROM ADAMS COUNTY, ILLINOIS.

*By Harry M. Hyatt. Alma Egan Hyatt Foundation, New York. \$6.00. 9½ x 6½; xvi + 723; 1935.*

An excellently indexed collection of superstitions and folk lore, including rhymes and riddles, gathered from the inhabitants of Adams County, Illinois. These are numbered and grouped under one hundred and sixty-five chapter headings dealing with nearly every conceivable familiar subject. In addition to an index by chapters, each of the 10,949 subjects in this book is alphabetically indexed.



#### THE GROWTH AND DISTRIBUTION OF POPULATION.

*By S. Vere Pearson. George Allen and Unwin, London. 12s. 6d. net. 9½ x 6; 448 + 1 plate; 1935.*

In spite of its title this prolix book is essentially Single Tax propaganda. Whatever the merits of the Single Tax we doubt whether it would prove to be such a panacea for population problems as Dr. Pearson thinks.



#### THE KATKARIS. *A Sociological Study of an Aboriginal Tribe of the Bombay Presidency.*

*By A. N. Weling. Bombay Book Depot, Girgaon, Bombay. 8½ x 5½; iv + 156 + 15 plates; 1934.*

An interesting study of the Katkaris, an aboriginal tribe of the Bombay Presidency. This book, with photographic illustra-

tions, gives a complete description of the country and the people; their physical affinities, their homes, their arts and sciences and their beliefs and rituals.



## ZOOLOGY

### THE ARACHNIDA.

By Theodore H. Savory. Longmans, Green and Co., New York. \$8.50. 9 $\frac{1}{2}$  x 7 $\frac{1}{2}$ ; xi + 218; 1935.

This is a well planned and well executed book on that somewhat neglected class of the Phylum Arthropoda, the Arachnida. The book is divided into three sections and an appendix. Part 1 discusses the general characteristics of the class as a whole; Part 2 describes the various orders, including fossil forms; and Part 3 is a review of different phases of the science of arachnology, which includes short chapters on economic, practical and historical arachnology. At the beginning of each chapter of Part 2 there is a diagnosis of about 100 words on the essential features of the order to be described, thus providing the means for a rapid survey of the characteristics of the whole class. The text is extremely well illustrated with outline drawings of at least one representative of each order, often supplemented with other line drawings of specialized structures, and in some cases still further supplemented with plates. Outline maps of the world show the distribution of the various orders of Arachnida. There are frequent tables of data that give a clean-cut air to the book. Mention should also be made of the author's "excursus" at the end of each chapter. This is usually about two pages in length and is generally an interesting little discourse on some particular feature of the class, such as "On Arachnid venom," "The spinning of Arachnida," "The tail and telson in Arachnida," "The Arachnida as formidable animals." The layman will find much of interest in this introduction to a fascinating group of creatures. For the zoölogist or naturalist it will also be a useful reference work.

In the appendix are extensive bibliographies, an *index rerum*, an *index auctorum* and an *index animalium*.

THE LONDON CONVENTION FOR THE PROTECTION OF AFRICAN FAUNA AND FLORA. *With Map and Notes on Existing African Parks and Reserves. Special Publication of the American Committee for International Wild Life Protection Number 6.*

American Committee for International Wild Life Protection, Cambridge. Free. 12 $\frac{1}{4}$  x 9 $\frac{1}{2}$ ; 48 + folding map; 1935 (paper).

The London Conference of 1933, called by invitation of the Government of Great Britain, was really a revival of the London Convention of 1900 which was never ratified. Representatives came to London from all of the countries having territories in Africa and there were "observers" from the Netherlands, India and the United States. The purpose of the convention was to institute a special regime for the preservation of rare or vanishing species of fauna and flora, particularly in Africa where they are in danger of extinction or permanent injury.

The text of the Convention as signed November 1933 is printed in full. The more important accomplishments are the defining and recommending of four types of parks and reserves and agreement aiming to control the commercial exploitation of animal products. An "Annex" contains illustrations and explanatory notes showing graphically the various mammals and birds recommended for special protection, and a 16-page table of African Game Reserves and National Parks, showing status and size of the various areas and the kind of game to be found in each. A large folding map shows the status of nature reserves in June 1935.

The terms of the treaty have been acceded to by Great Britain, Belgium and Egypt. When one more country signs up, the four signatures necessary for ratification will have been obtained, and then this important treaty will be able to function.



### PARADE OF THE ANIMAL KINGDOM.

By Robert Hegner. Assisted by Jane Z. Hegner. The Macmillan Co., New York. \$5.00. 10 $\frac{1}{2}$  x 7 $\frac{1}{2}$ ; vi + 675; 1935.

The reader of this delightful contribution to the lively sciences stands on the gang-



plank of Noah's Ark and watches the animal kingdom file past him, from the lowly *Amoeba* to the almost human gorilla. The last member of the parade is omitted for the obvious reason of lack of space. The animals described include members of each of the large divisions of the animal kingdom, and have been chosen because they are familiar in everyday life or in literature, because they are economically important, or because they are commonly seen in circuses and zoos. The reader learns what they look like, where they live, how they protect themselves, obtain their food, and reproduce and what their effect is on human welfare. Nor is the folklore of animals neglected. The book contains 743 excellent illustrations, most of them photographs of the living animals in their native habitats. There is a detailed index. We know of no more attractive introduction for either children or adults to the fascinating study of our animal cousins.



AN INTRODUCTION TO COMPARATIVE ZOOLOGY. *A Text-book for Medical and Science Students.*

By F. G. Sarel Whitfield and A. H. Wood.

P. Blakiston's Son and Co., Philadelphia.

\$5.00. 9 $\frac{1}{2}$  x 7 $\frac{3}{4}$ ; x + 354; 1935.

It is the viewpoint of the authors that the usual zoology courses and texts are not properly organized and developed from the point of view of the medical student who must, in his preparation, have contact with the subject but should be privileged to miss certain details and minutiae which are adjudged irrelevant. Accordingly they have written for the medical student the present volume on zoology, stressing the evolutionary and comparative viewpoint. Actually, the book seems quite orthodox in its general scope. It is divided into two parts: the first section deals with a phylum-by-phylum review of the principal animal groups, and the second section stresses biological principles—metabolism, heredity, evolution, and ecology. The book does omit much material which could only be superfluous to the young medico and stresses, wherever

practicable, the human aspects of the subject. It is rather curious that in the chapter on ecology the entire emphasis is placed on the old "web of life" idea. The text is supplemented by a number of original illustrations which are definitely helpful. There is a brief glossary and an index.



FAUNA OF THE NATIONAL PARKS OF THE UNITED STATES. *Wildlife Management in the National Parks. United States Department of the Interior, Contribution of Wildlife Division, Fauna Series No. 2.*

By George M. Wright and Ben. H. Thompson. U. S. Government Printing Office, Washington. 20 cents. 9 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; viii + 142; 1935 (paper).

Although the title implies that this small book is simply an annotated list of the animals inhabiting our National Parks, inspection of the contents shows this is not the case. The book presents some new life-history data and general observations on the fauna of the Parks, but seems largely interested with the important problem of wild-life conservation and management. This can be stated in the words of the authors, who say: "Viewing the volume as a whole, it is evident that it deals with wildlife management and makes no pretense of presenting new facts in the form of pure zoology."

The book is divided into two parts. Part I is entitled, "Perpetuation and utilization of primitive wildlife values," and Part II, "Present status of national parks wildlife and the restoration program."

Naturalists, conservationists, and wildlife administrators will find the book useful.



LES INVERTÉBRÉS. *Arthropodes, Mollusques et Échinodermes. Actualités Scientifiques et Industrielles, 242. Leçons de Zoologie et Biologie Générale, IV.*

By Georges Bobn. Hermann et Cie, Paris. 18 francs. 10 x 6 $\frac{1}{2}$ ; 132; 1935 (paper).

This volume, the fourth of the series dealing with the invertebrates, concerns

itself with the arthropods, molluscs, and echinoderms. The book starts off in a conventional manner by discussing the principal characteristics of the phylum Arthropoda and stressing the serial homology between the various arthropod types. Following this are brief considerations of the comparative anatomy of insects and crustaceans; the biology of the crustaceans; the reproduction and development of insects; insect parasites; the instincts of insects; the arachnids; the molluscs and the echinoderms.

In some ways this book is better than its predecessors yet it leaves much to be desired by the serious student of invertebrate zoölogy. These books seem sketchy and leave out much information that should be included. One gets the impression that they have been hurriedly assembled and do not represent the expenditure of great time and energy in their preparation.



**LE POLYMORPHISME DES MALES DE COLÉOPTÈRES.** *Actualités Scientifiques et Industrielles*, 255. *Exposés de Biométrie et de Statistique Biologique*, VI.

By **Renaud Paulian.** *Hermann et Cie, Paris.* 10 francs. 10 x 6½; 35; 1935 (paper).

Polymorphism among insects is not an infrequent phenomenon. It is especially well exhibited by certain of the beetles, e.g. the Lamellicorns, where the males frequently possess grotesquely produced mandibles and various dorsolateral head excrescences. The author of this short monograph has examined many of these structures biometrically and comes to the conclusion, already prevalent, that the explanation for the multiplicity of form with respect to certain anatomical characters is as yet "far from being explained." He does conclude, however, that the polymorphic structures of the Coleoptera can be divided into two categories; trophic or constant variants, characters which vary little between individuals, and genetic or inconstant variants which display more inter-individual variation. This interesting little book is a worthy addition to the "*Actualists*" series.

**MIGRATIONS ET MÉTAMORPHOSES DE L'ANGUILLE D'EUROPE.** *Actualités Scientifiques et Industrielles*, 264. *Exposés de Biologie Zoologique*, II.

By **Léon Bertin.** *Hermann et Cie, Paris.*

15 francs. 10 x 6½; 57; 1935 (paper).

This is an interesting account of the various stages in the life cycle and the migrations of the European eel. Born in the Sargasso Sea as transparent pelagic larvae called Leptocephales, they migrate in that stage to the coastal waters of Europe via the Gulf Stream. There they become transparent eels and invade the inland seas and fresh waters. They undergo two other metamorphoses—first into the yellow eel and then into the silver—before starting their reproductive migration back to the Sargasso Sea. It is estimated that they travel at the rate of 13 to 30 kilometers a day, depending upon such factors as length of day, temperature and salinity of the water. The work is illustrated with photographs, drawings, and maps, and has a bibliography of three pages.



**WEST COAST SHELLS.** *A Description in Familiar Terms of the Principal Marine, Fresh-Water, and Land Mollusks of the United States, British Columbia, and Alaska, Found West of the Sierra.*

By **Josiah Kest.** Revised by **Joshua L. Bailey, Jr.** *Stanford University Press, California.* \$3.75. 7½ x 5½; xi + 350; 1935.

The first edition of this minor classic appeared in 1887, and two revisions have preceded the present one which brings up to date the nomenclature and descriptions of species of marine shells ranging from Alaska to San Diego, and of land and fresh-water forms in Washington, Oregon and California. There are 334 figures—pen and ink drawings—to aid in identification. The index lists specific and varietal names alphabetically under the genera. The book is written in an informal, interesting style and the student of conchology may well thank Mr. Bailey for this careful revision of a useful handbook.

FROGS, TOADS, AND SALAMANDERS. *Science Guide for Elementary Schools, Volume 1, Number 6.*

By Edith A. Pickard. Division of Text-books and Publications, California State Department of Education, Sacramento. 15 cents. 9 x 6; iii + 55; 1935 (paper).

This is a guide for teachers in the grade schools who know little about biology but wish to awaken some interest for natural science in their pupils. Special reference is made to California species of amphibians, but the guide can be used with advantage in any locality. The life histories and characteristics of the amphibians are briefly outlined. Directions for making a vivarium and a few simple experiments to perform on the living frog are suggested. The pamphlet should be helpful.

FAMILIAR BIRDS OF THE PACIFIC SOUTHWEST with Size and Color Key.

By Florence van V. Dickey. Stanford University Press, Stanford University, Calif. \$3.75. 6½ x 4½; lviii + 241; 1935.

This book was written with the sole object of enabling the amateur to identify birds easily and quickly. By noting the size in comparison to a few well-known birds and the predominant color, one can make a fair shot at naming 201 birds. Short descriptions of many birds are given and there are over 100 beautifully colored plates. There is a good index and a check list of scientific and common names.

A MANUAL OF LAND AND FRESH WATER VERTEBRATE ANIMALS OF THE UNITED STATES (Exclusive of Birds). Second Edition.

By Henry S. Pratt. P. Blakiston's Son and Co., Philadelphia. \$6.00. 9 x 6; xvii + 416 + folding map; 1935.

The main purpose of the revision of this Manual has been to reflect in it the numerous changes in the nomenclature of the vertebrate animals of the United States which have been made in the past few years, and to define more precisely their known ranges of distribution. Dr. Em-

mett Reid Dunn, Professor of Biology in Haverford College, has thoroughly revised the sections on Amphibians and Reptiles.



ENTOMOLOGY. With Special Reference to Its Ecological Aspects. Fourth Revised Edition.

By Justus W. Folsom. Revised by R. A. Wardle. P. Blakiston's Son and Co., Philadelphia. \$4.00. 8½ x 5½; ix + 605; 1934.

This fourth edition has been prepared by Professor Wardle. While no changes have been made in the basic structure of the book and those features in the previous editions which appealed to teachers and students have been retained, a great amount of new matter has been interpolated throughout and several chapters have been remodeled, notably those dealing with Insects and Disease and Insects and Man.

THE JUVENAL PLUMAGE AND POSTJUVENAL MOLT IN SEVERAL SPECIES OF MICHIGAN SPARROWS. Bulletin No. 3.

By George M. Sutton. Cranbrook Institute of Science, Bloomfield Hills, Mich. 50 cents. 9 x 6; 36 + 8 plates; 1935 (paper).

The author defines and describes more clearly than has heretofore been done the juvenal and postjuvenal plumage in birds. His discussion is based on observations made during a six-weeks study of bird life on the Edwin S. George Wild-Life Reserve. There are excellent descriptions and illustrations of the plumage of eleven different species of sparrows.

THE SPRUCE BUDWORM ON MICHIGAN PINE. University of Michigan, School of Forestry and Conservation, Bulletin No. 6.

By Samuel A. Graham. University of Michigan Press, Ann Arbor. 25 cents. 9 x 6; 36; 1935 (paper).

This bulletin describes briefly the recent

rather serious outbreaks of the spruce budworm which is now attacking the jack pine in the Lake States. In some detail the life history of the insect, the influence of environment on the population, and specific measures for future control are discussed.



ANIMALIUM CAVERNARUM CATALOGUS.  
Pars 2, 3, 4, 5, 6.

By Benno Wolf. W. Junk, Berlin and 's-Gravenhage. Single copy 18 marks (Holland: Fl. 10.60); subscription price 13.50 marks (Holland: Fl. 8). 10 x 7½; 128 pages each; 1934-1935 (paper).

The first number of this thorough and systematic catalogue of the cavern fauna of the world was noticed in Volume 10, page 104 of this REVIEW. These numbers include lists of authors from Ch to No; caves in Germany, France, Greece and Italy; and the phylum Arthropoda.



A CLASSIFICATION OF FISHES. Including Families and Genera as Far as Known. Stanford University Publications, Biological Sciences, Volume III, Number 2.

By David Starr Jordan. Stanford University Press, California. \$3.50 (paper); \$4.25 (cloth). 10 x 6½; 163 + x, 1934 (second printing by photolith).

This is a photolithographic reprint of a well-known work, originally published in 1923, by one of America's greatest ichthyologists.



THE MANGROVE WARBLER OF NORTH-WESTERN MEXICO. *Transactions of the San Diego Society of Natural History*. Volume 8, Number 10.

By A. J. van Rossem. *Society of Natural History, San Diego, Calif.* 10½ x 6½; 2; 1935.

A NEW RACE OF BROWN TOWHEE FROM THE INYO REGION OF CALIFORNIA. *Transactions of the San Diego Society of Natural History, Volume 8, Number 11.*

By A. J. van Rossem. *Society of Natural History, San Diego, Calif.* 10½ x 6½; 3; 1935.

A NEW SILKY POCKET MOUSE FROM SONORA, MEXICO. *Transactions of the San Diego Society of Natural History, Volume 8, Number 12.*

By Laurence M. Huey. *Society of Natural History, San Diego, Calif.* 10½ x 6½; 2; 1935.

A NEW SUBSPECIES OF CROTALUS CONFLUENTUS, THE PRAIRIE RATTLESNAKE. *Transactions of the San Diego Society of Natural History, Volume 8, Number 13.*

By Laurence M. Klauber. *Society of Natural History, San Diego, Calif.* 10½ x 6½; 13 + 1 plate; 1935.

NEW OR LITTLE KNOWN CRABS FROM THE PACIFIC COAST OF NORTHERN MEXICO. *Transactions of the San Diego Society of Natural History, Volume 8, Number 14.*

By Steve A. Glassell. *Society of Natural History, San Diego, Calif.* 10½ x 6½; 20; 1935.

A NEW GENUS AND SPECIES OF PYGMY GOOSE FROM THE MCKITTRICK PLEISTOCENE. *Transactions of the San Diego Society of Natural History, Volume 8, Number 15.*

By Roland C. Ross. *Society of Natural History, San Diego, Calif.* 10½ x 6½; 7; 1935.



BOTANY

WEEDS.

By Walter C. Muenscher. *The Macmillan Co., New York.* \$6.00. 8½ x 5½; xxii + 577; 1935.

If a large-scale campaign of weed eradication or control is to be both effective and economical the first step, according to Muenscher, should be the identification of the offending plant for the purpose of facilitating the selection of the most vulnerable part of the plant against which to launch an attack. He has skillfully adapted this reference book to the needs of people in diverse walks of life who have to contend with plants that grow where they are not wanted. While it can be most readily used by people with botanical training a series of more than a hundred excellent drawings make it possible to

find the names of more than that number of plants merely by leafing through the book. There is a dichotomous key based on morphological characters for the identification of 500 common weeds infesting the northern part of the United States. Each species has a botanical description, notes on its distribution and the kind of situation in which it is likely to be troublesome, and recommendations for eradication or control. Most of the species and practically all of the genera are represented by excellent drawings showing the mature plant, flower, seed, seedling, and any other organs important in propagation. The excellent introductory sections, covering 90 pages, discuss the special characteristics of weeds, the weeds of special habitats, the control of weeds by means of the usual agricultural practices, and the control of weeds by chemical means. There is a very good index, an extensive bibliography and an adequate glossary.



#### CHRONICA BOTANICA. Volume I.

*Edited by Fr. Verdoorn. Chronica Botanica, P. O. Box 8, Leiden, Holland. 15 Neth. guilders. 9½ x 6½; 447; 1935.*

In this year-book plant science has a new and unique annual, about which Professor E. D. Merrill, in an introductory chapter says:

The "Chronica Botanica" as conceived covers a field not hitherto pre-empted, conflicts with no established periodical, supplements those already in existence, and should, by its very nature, encourage the spirit of international coöperation, a spirit characteristic of this our science, of which we, as botanists representing all nations, are individually and collectively proud.

The chief feature of the new year-book is a review of the important current research in all branches of plant science—agronomy, forestry, horticulture, microbiology, soil science, agricultural chemistry, etc.—throughout the world. Other features are: Illustrated professional and personal news of the past year, with notes about future events; an index of main acquisitions of herbaria, botanic gardens, etc.; reports and notes on the societies and congresses; an exhaustive and up-to-date list of institutions, societies and workers

There is an index of plant names and plant parasites and an index of persons.



#### THE ALGAE AND THEIR LIFE RELATIONS. *Fundamentals of Phycology.*

*By Josephine E. Tilden. University of Minnesota Press, Minneapolis. \$5.00. 9½ x 5½; xiii + 550 + 1 plate; 1935.*

The need for a textbook in the field of phycology has been a crying one. This is well pointed out by Doctor Tilden, who says in the preface to her book:

Phycology offers an enormously stimulating field for research, but the teaching of it is likely to have results that are far from satisfactory. At present there is no textbook that will do duty as a guide to the student and at the same time supplement the lectures and the laboratory and field work which a conscientious teacher feels should be made available to him. Reference books for experienced investigators are not lacking; among recent publications in this country and abroad are several excellent works dealing exhaustively with some special phase of the field, such as blue-green algae, green algae, fresh-water algae, and taxonomic studies of individual groups of algae. No textbook is obtainable, however, which answers for the thinking student the questions, Are there connecting links between the several classes of algae? Is there a relationship between any of the classes of algae and the higher plants, or between the algae and the primitive or the higher animals? What is the probable place of origin or point of unusual development of any particular algal group with respect to the geological history of the world?

... The object in preparing the present volume has been to offer to teachers and students material arranged in orderly fashion, on the basis of which any desired course may be planned. Terms have been simplified and reduced in number; a series of life cycle diagrams have been included with the object of clarifying many things that in the past have seemed meaningless. The key to the system of arrangement and classification is based on a limitation of the use of the term "spore."

In the opinion of the reviewer this book meets the problems and ideals discussed in the preface and will undoubtedly be welcomed by botanists generally. The book is well illustrated and has a bibliography and an index.



#### A TEXTBOOK OF BACTERIOLOGY.

*By Thurman B. Rice. W. B. Saunders Co., Philadelphia. \$5.00 net. 9½ x 6; 551;*

In his practice the clinician frequently wishes to review certain points about medical bacteriology. He may wish to merely learn the latest and accepted name of an organism, or he may want quick and practical advice on the availability and efficacy of specific biological products in the treatment of a malady. This book is designed to help the clinician deal with such problems by summarizing much of the existing knowledge on the bacteriology of disease. The author attempts to give the following information about the more important diseases: historical remarks; morphological and cultural characteristics of the organism; pathogenicity and lesions produced; specific biological products and their value in treatment, and prophylactic measures. There are also chapters on bacterial culture technique and the theoretical aspects of immunity. A few illustrations and an adequate index are to be found but there is no bibliography. The book should find supporters among the group for which it was written.



BRITISH STEM- AND LEAF-FUNGI (CORLOMYCETES). *A Contribution to Our Knowledge of the Fungi Imperfecti Belonging to the Sphaeropsidales and the Melanconiales. Volume I. Sphaeropsidales. To the end of the Sphaerioidae which have colourless or nearly colourless spores.*

By W. B. Grove. *The University Press, Cambridge; Macmillan Company, New York.*  
\$7.00. 8½ x 5½; xx + 488; 1935.

Students of the Fungi Imperfecti will welcome the appearance of this monograph. Many North American species are included.

The present volume includes all the British Sphaeropsidales to the end of the Scolecosporeae; the remainder of them and the Melanconiales, which embrace species of greater beauty and complexity, will form a second volume of about the same size.

The account given of each species is in the main purely morphological; few pathological or cultural details are included, except very briefly. This is intentional. The two departments of Mycology, as experience many times has shown, are best treated by specialists, but working in happy conjunction.

Description of each species is accompanied by critical taxonomic notes, eco-

logical data, and the name of the host plant on which it has been found. There is an index of the genera of host plants mentioned in this book and an index to the fungi described. Latin descriptions of 24 new species are given in an appendix.



EVOLUTION OF FOLIAR TYPES, DWARF SHOOTS, AND CONE SCALES OF PINUS With Remarks Concerning Similar Structures in Related Forms. *Illinois Biological Monographs, Vol. XIII, No. 3.*

By Clifton C. Doak. *University of Illinois Press, Urbana.* \$1.50. 10½ x 6½; 106; 1935 (paper).

A study of the axial and foliar systems of about thirty-five species of pines and of a few related plants. The ontogeny of the cotyledons supports the view that polycotyledony is a primitive character and that fusions, incorporations, and reductions mark advances. A technique is described whereby the number of bud scales and of sterile bracts can be approximately determined prior to extension of the buds which contain them. The technique is utilized in following the time of origin of units within the bud. Most of the unique vegetative characters of *Pinus* can be directly or indirectly attributed to influences incident to the formation of the compound bud. This structure relieved the sheath scales from the work of meristematic protection and permitted specialization along other lines. It necessitated the almost simultaneous development of many structures from stored food and exerted shaping pressures upon the enclosed immature dwarf shoots.

Numerous illustrations, diagrams, tables, and a bibliography of 105 titles, are included in the study.



CACTUS GROWING FOR BEGINNERS.

By Vera Higgins and H. T. Marrable. *The Blandford Press, London.* 2s. 6d. net. 7½ x 5½; 84; 1935 (paper).

Mrs. Higgins, an expert in cactus growing, has enlisted the aid of an amateur in the field "who has made every mistake a

beginner could make, and who should therefore be in a position to appreciate just how much and how little a beginner knows," in the preparation of this handbook for members of the English Cactus and Succulent Society and other cactus raising fans and collectors. Descriptions are given of the more common types of cacti, with detailed instructions for their cultivation in homes and greenhouses. In a final chapter, "Summary of Operations," is reviewed the work to be done with these remarkable plants at different seasons of the year. The booklet is adequately indexed.



A TEXTBOOK OF GENERAL BACTERIOLOGY.  
*Eleventh Edition, Entirely Reset.*

By Edwin O. Jordan. W. B. Saunders Co., Philadelphia. \$6.00. 9 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; 825; 1935.

Although a new chapter on bacterial variation has been added and many portions have been rewritten to bring it up to date, this well-known standard textbook remains much the same as in earlier editions. It presents a very comprehensive survey of bacteriology assuming no knowledge on the part of the reader. While the bulk of the book is concerned with forms pathogenic to man, there are also chapters on the nitrogen cycle, bacteria in industry, bacteria of the air, soil, and water, and bacterial diseases of plants. There is an excellent index subdivided into "authors" and "subjects." A fair number of references are given as footnotes, but there is no general bibliography.



THE HERBACEOUS FLOWERING PLANTS (*Exclusive of Grasses and Sedges*) Growing Without Cultivation in the Vicinity of Orono, Maine. *University of Maine Studies, Second Series, No. 34.*

By Eugene C. Ogden. The University Press, Orono, Maine. \$1.00 (bound); 50 cents (paper). 8 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; 77; 1935.

This "annotated list of the herbaceous flowering plants (exclusive of grasses and sedges) which have been found growing

without cultivation within the towns of Old Town, Orono, Veazie, Bradley, and Milford, including some plants which though considered woody might be looked for in this list," is based on the recent collections of the author and upon examination of specimens in the Gray Herbarium and other herbaria. Brief taxonomic and ecological notes accompany the list of 623 plants. There is a topographic map of the region and there is an index of popular and scientific names.



HVALRÅDETS SKRIFTER. *Scientific Results of Marine Biological Research. Nr. 10. The "Qst" Expedition to the Denmark Strait 1929. II. The Phytoplankton and its Conditions of Growth (Including Some Qualitative Data from the Arctic in 1930).*

By Trygve Braarud. Edited by Universitetets Biologiske Laboratorium. Jacob Dybwad, Oslo. 10 $\frac{1}{2}$  x 7; 173; 1935 (paper).

This publication includes a very thorough discussion of the different factors governing phytoplankton production in the sea, emphasis being placed on the factors which influence the number of plants. A description is given of the vegetation and conditions of plant production in the Atlantic, Arctic and Polar water masses of the Denmark Strait. A list of all species is given together with valuable notes on their distribution and taxonomy.



PLANT VIRUSES.

By Kenneth M. Smith. Methuen and Co., London. 4 shillings net. 6 $\frac{1}{2}$  x 4 $\frac{1}{2}$ ; ix + 107; 1935.

In this little volume (of the series of Methuen's Monographs on Biological Subjects) is presented in a brief but understandable way some of the more interesting and important facts concerning plant viruses. Botanists and entomologists will find problems of fundamental importance in their own field such as the "affinities of viruses with enzymes, their intimate relationship with the living cell, their curious and interesting association with insects, and finally the possibility that

they may represent a new and simple form of life." The volume is illustrated, contains a list of 94 references and is indexed.



**AMERICAN FERNS.** *How to Know, Grow and Use Them.*

By Edith A. Roberts and Julia R. Lawrence.  
The Macmillan Co., New York. \$2.50.

9½ x 6½; viii + 98; 1935.

This book tells how to identify ferns, how to raise them from spores, and which ones are best for use in various types of gardens. It contains many beautiful photographs and a good index.



## MORPHOLOGY

**PRINCIPLES OF INSECT MORPHOLOGY.**

By R. E. Snodgrass. McGraw Hill Book Company, New York. \$6.00. 7½ x 5½; ix + 667; 1935.

Not so very long ago insect morphology was a comparatively unexplored science. Entomologists were familiar, of course, with the general principles of insect structure but little knowledge was available about the finer anatomical details. This book by Doctor Snodgrass serves the twofold purpose of putting insect anatomy on a respectable basis and of integrating much of the work done by recent investigators. Just as students of human anatomy refer to "Gray," entomologists will find themselves seeking "Snodgrass" when they wish information on some detail of insect anatomy. It is not the purpose of the reviewer to imply that the present volume is complete in the sense that all structural systems are perfectly worked out. This is not the case; there still remains much work to be done. The book, however, is an important advance towards that end.

The subject matter is presented in a standardized but effective manner. Typically, a chapter is devoted to a particular structural system although in some instances more space is needed. The functional viewpoint is admirably stressed so that the reader gets a good idea of the use of structures as well as an understanding

of their anatomy. A glossary of terms applying to the material just discussed is appended to each chapter. A selected bibliography, an index, and many illustrations increase the value of the text.

This book is a welcome and important addition to zoological literature.



**ELEMENTARY MICROTECHNIQUE.**

By H. Alan Peacock. Longmans, Green and Co., New York. \$1.90. 7½ x 4½; vii + 200; 1935.

A book designed primarily for beginning students of histology and cytology with the purpose of filling the gap between the instruction sheets of the classroom and the larger reference volumes. A brief résumé of the structure of the cell and protoplasm and short descriptions of the processes of microtechnique and the principles they involve are followed by a chapter outlining methods and technique. Included here in tabular form are notes on the general character, use and effects of about twenty of the most commonly used fixatives. Listed alphabetically and quite adequately for their purpose in three separate chapters are: (1) subjects for special study with the steps of various methods to be followed in their preparation; (2) stains and their uses; (3) formulae and hints. There is an index and three appendices, including a bibliography, information on the sources and culture of several materials, and methods for the preservation of materials.



**THE MICROSCOPIC ANATOMY OF VERTEBRATES.**

By George G. Scott and James I. Kendall. Lea and Febiger, Philadelphia. \$3.75. 9½ x 5½; 306; 1935.

A college textbook designed to accompany laboratory work in the field of vertebrate histology and microscopic anatomy, the work to be covered in one semester. After an introductory chapter on the cell and embryology the topics treated are: epithelial tissues; connective tissues; blood; muscle tissues; nerve tissue; vascu-



lar system; lymphatic system; integument; respiratory system; digestive system; excretory system; female reproductive system; male reproductive system; and endocrine glands. The final chapter gives detailed information on technique. A list of references is given at the end of each chapter and in an appendix will be found lists of current references, anatomical and histological texts, also a lengthy list of prepared slides to be used in the course. The volume is well illustrated and is indexed. A highly useful book for teaching purposes.



THE ANATOMY OF THE NERVOUS SYSTEM. *From the Standpoint of Development and Function. Fifth Edition, Revised.*

By Stephen W. Ranson. W. B. Saunders Co., Philadelphia. \$6.50.  $9\frac{1}{8} \times 6\frac{1}{2}$ ; 501; 1935.

Recent work in neurology has made necessary a revision of many of the important concepts presented in the earlier editions of this useful text. However, the complexity and mass of material has not been extended, as the author feels that the student of neurology can absorb only very definite amounts of detail. The most important change has been in the part discussing the central visual pathway. The text in this revised form is certainly one of the most accurate and easily comprehensible texts available for medical students.



INTRODUCTION TO VERTEBRATE EMBRYOLOGY. *A Textbook for Colleges and Universities. Third Edition, Revised and Enlarged.*

By Waldo Henshaw. John Wiley and Sons, New York. \$4.00 net.  $9 \times 5\frac{1}{2}$ ; xii + 390; 1935.

The first edition of this successful textbook was reviewed in Vol. 3, No. 1, and the second edition in Vol. 6. The first half of the text in this new edition has been entirely reorganized and rewritten. In fact the only section that has remained in its old form (except for the addition of some new illustrations) is Part III dealing with organogeny.

## PHYSIOLOGY AND PATHOLOGY

### SIX CONFÉRENCES DE PHYSIOLOGIE.

By Léon Binet. Masson et Cie, Paris. 12 francs.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; 73; 1935 (paper).

### LEÇONS DE PHYSIOLOGIE MÉDICO-CHIRURGICALE.

By Léon Binet, with the collaboration of MM. Arthus, E. Benhamou, R. Fabre, J. Huguenaud, Mme C. Jéramet, MM. J. Gosset, M. Kaplan, J. Marie, J. Patel, A. Sicard, and M. Sureau. Masson et Cie, Paris. 40 francs.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; 245; 1935 (paper).

The first of these books by a distinguished physiologist contains six lectures delivered before the Faculty of Medical Sciences at Buenos Aires, in August and September, 1934. The titles are: (1) What is a lung?; (2) New biological and therapeutic investigations on asphyxia; (3) Adrenals and glutathione; (4) Provoked hyperthermia (humoral syndrome); (5) Some investigations on nerve; (6) The biologically reactive fish.

The second is a collection of lectures presented by the author and some of his colleagues in a weekly course inaugurated by him in the hospital services of Paris. A wide range of topics was offered. Included among them were reanimation; the physio-pathology of arterial embolism; the functional exploration of the spleen; acute nephritis; the biological diagnosis of pregnancy. The general impression we get is that the meetings must have been highly successful and stimulating.

In the first of these books each lecture is provided with a bibliography; in the second some are documented. Both are illustrated.



A CONTROLLED EXPERIMENT ON RURAL HYGIENE IN SYRIA. *A Study in the Measurement of Rural Culture Patterns and of Social Forces.*

By Stuart C. Dodd. American University, Beirut, Lebanon. \$2.00 net.  $9\frac{1}{8} \times 6\frac{1}{2}$ ; xv + 336 + 12 plates and folding map; 1934 (paper).

This is the report of an investigation which had for its main object the development of a method of measuring the hy-

gienic conditions of Syrian villages. The means by which the information was obtained, the form of questionnaire used and the estimation of errors are discussed in great detail. Praiseworthy are the efforts of the author to determine and measure the errors which might affect the reliability of his results, but the statistical analysis is perhaps excessively refined considering the nature of the material and size of samples.

The author's method received practical application in an attempt made to measure the effect of health instructions on hygienic conditions. Four Syrian villages were surveyed and the hygienic status of the inhabitants measured. One village was selected as experimental and for two years the natives were given instructions by an itinerant clinic.

After this period the experimental village and the three control villages were resurveyed. This second survey showed that the experimental village had made a progress estimated at 20 per cent, while the average score of the control villages had gained by 18 per cent. This equal progress, which is regarded as statistically significant, according to the author is due to the fact that the inhabitants of the control villages were in some contact with those of the experimental village and therefore benefited by the instructions given in the latter. The question that one would like answered at this point is: Did the morbidity actually decrease in these villages?



LE SECR DEBT LA VIE. *Les Ondes cosmiques et la Radiation vitale. Deuxième édition revue et augmentée de "L'Origine de la Vie."*

By Georges Lakhovsky. Gauthier-Villars et Cie, Paris.  $7\frac{3}{4} \times 5\frac{1}{2}$ ; xxi + 261 + 6 plates; no date (paper).

L'OSCILLATION CELLULAIRE. *Ensemble des Recherches Expérimentales.*

By Georges Lakhovsky. Gaston Doin et Cie, Paris. 40 francs.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; 319; 1931 (paper).

According to Lakhovsky every cell contains elements of oscillating electric circuits which absorb and emit electromag-

netic radiations. Health and disease are dependent upon the equilibrium or disequilibrium between the rays absorbed and the rays emitted. This theory was first put forth at length by him in *L'Origine de la Vie* noticed in Volume 3, page 433 of this REVIEW. The first of the books noticed now is a second, augmented edition of this work. Three chapters have been added: Influence of sun spots on life and health; Influence of the nature of the soil on the field of cosmic rays; Contribution to the etiology of cancer; and the therapeutics of cellular oscillation.

The second book is a collection of papers by the author and reviews of his work by Auguste Lumière, Artij, Rivera and other workers who are apparently sympathetic with Lakhovsky's theory. The discussions on cancer are amplified to a greater extent than in the *Secret de la Vie*. They are more interesting than convincing.



CELSUS DE MEDICINA. [In two volumes]. Volume I.

With an English Translation by W. G. Spencer. Harvard University Press, Cambridge. \$2.50 (cloth); \$3.50 (leather).  $6\frac{1}{2} \times 4\frac{1}{2}$ ; xiv + 499; 1935.

Nobody knows much about who or what the person who wrote this treatise was. It is not certain that he ever practised medicine, or had any closer relation to it than to write extremely well about it. It has indeed been suggested that Celsus only translated and adapted a pre-existing Greek treatise, perhaps by Cassius, perhaps by Titus Aufidius Siculus, who was a pupil of Asclepiades. But in any case it is an extremely interesting book. It starts off with an excellent, if brief, history of medicine up to the time (roughly the reign of Tiberius). This is followed by general considerations of disease and treatment, and in turn the discussion of particular diseases. The first four books are included in this volume, to be followed by a second completing the work.

The translation and notes are excellent, satisfactorily maintaining the high stand-

ards of the Loeb Classical Library. It will be a valuable addition to any medical or biological library.



**THE DISEASES OF THE ENDOCRINE GLANDS.**  
*Third Edition, Revised and Enlarged.*

By Hermann Zondek. Translated by Carl Frausnitz. William Wood & Co., Baltimore. \$11.00. 9½ x 6½; xi + 492; 1935.

This book is an English translation of the third German edition. The scope of the volume can be expressed in the author's own words:

It was not so much my aim to make the book a compendium of all the physiological data and opinions comprised in the enormously developed subject of endocrinology; rather was it my intention that it should remain what it had been in the past: primarily a book for the clinician.

The text is divided into two sections: part I, a general discussion about the physiology, pharmacology and interrelations of the endocrines and their hormones, and part II, a discussion of specific pathologies and diseases due to endocrine aberrations.

This is a scholarly and workable text on clinical endocrinology and its appearance in English is welcome. The author is admirably wary of advocating radical and untested methods of treatment for glandular disorders. For this reason, the book is an important opponent of the "quack" type of endocrinology which is all too prevalent today. There is a detailed bibliography and a useful index.



**A NEW ANGLE ON HEALTH.** (*Nature's Provision for the Health and Happiness of Mankind*).

By D. H. C. Given. John Bale, Sons and Danielsson, London. 7s. 6d. net. 9½ x 6; xvii + 160 + 5 plates and 3 folding tables; 1935.

As far as the reviewer can perceive the thesis of this book runs as follows: With civilization the human race has so altered its biological environment that two great

categories of diseases have sprung up, the "diseases of poverty" and the "diseases of riches." The former are the result of inadequate living and social conditions, e.g., overcrowding, malnutrition, insufficient sunshine, etc. The latter result from "self-indulgence before temperance" where certain organs are overworked and others are underworked, thus throwing the body "out of gear." The author claims that about 80 per cent of the total mortality is directly or indirectly attributable to these two "diseases." The remedy lies first in simply altering, improving and intellectualizing conditions among both rich and poor, and, second, in the words of the Bible and the author, "Seek ye first the kingdom of God (meaning Nature, God's kingdom upon earth) and all these essential things will be added unto you." A naïve book.



**EXPERIMENTAL PHYSIOLOGY.** *With Anatomical and Mechanical Illustrations and an Appendix of Technical Data.*

By Maurice B. Visscher and Paul W. Smith. Lea and Febiger, Philadelphia. \$3.25. 9½ x 5½; 191; 1935.

In this book laboratory experiments in general and mammalian physiology are outlined for the medical student. Many of the experiments are classical in nature and, as the authors point out, are not included because of especial originality but because of their importance in the understanding and interpretation of animal function. Exercises are outlined which cover such topics as the general properties of protoplasm, and the mechanism of muscular activity, circulation, respiration, nervous activity, digestion, metabolism and excretion. The book is tersely written, the assumption presumably being that the student using it will have both a considerable background in physiology and opportunity for facile consultation with his instructors. A pertinent reference at the end of each experiment aids the student in collateral reading if he so desires. There is an appendix of useful formulae and an adequate index.

## PUBLIC HEALTH ADMINISTRATION IN THE UNITED STATES.

By Wilson G. Smillie. *The Macmillan Co., New York.* \$3.50.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; xvi + 458; 1935.

A timely and highly useful book. The author has compiled "the material that is available concerning the administrative aspects of public health organization and procedure and has attempted to correlate one activity with another, and fit each into its proportionate place; to present an analysis of present practices, and suggest probable future developments." It is pointed out that public health work must always be dynamic—not static—and that this book is not to be regarded as an authority but simply as a guide. The main part of the volume is divided into three sections. The first deals with administrative control of communicable diseases that are commonly encountered in public health practice; the second with basic activities of a health organization; and the last with organization of public health programs. Figures, graphs and charts illustrate salient points in the book. A list of references accompanies each chapter and a detailed index is given.

NUTRITION WORK WITH CHILDREN. *Revised and Enlarged Edition.*

By Lydia J. Roberts. *University of Chicago Press, Chicago.* \$3.50.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; xix + 639; 1935.

The advances made in nutritional fields have been so great in the last decade that the author has found it necessary to develop a new and completely revised edition of this book in order to bring the material up to date and to correct certain errors of the first edition. The following new discussions have been added: first, a consideration of the effects of the depression on nutrition and health; second, a consideration of the distinctions between the adequate and optimal nutrition of children; third, an expansion of the discussion on the mental effects of undernutrition; fourth, a discussion of high school health problems, and, last, a critique of the rôle played by various national and local

agencies and programs in affecting the health and nutrition of children.

This book is well written, contains detailed bibliographies following each chapter, and is thoroughly scientific in its viewpoint.

THE PHYSIOLOGY OF DOMESTIC ANIMALS. *Third Revised Edition.*

By H. H. Duker. *With a chapter on The Physico-Chemical Basis of Physiological Phenomena, by E. A. Hewitt. A part on Reproduction, by G. W. McNutt. Comstock Publishing Co., Ithaca, N. Y.* \$6.00.  $9 \times 6$ ; xiv + 643; 1935.

The first two editions of this book were lithoprinted. The demand for the text has been sufficient to bring the book out as a printed edition and to change its format generally. The material has been thoroughly revised by altering and rewriting much of the text and by changing a number of the illustrations. The aims and scope of the book, however, remain fundamentally unchanged. The book has been designed primarily to serve as a reference volume for the veterinarian although it should be useful, in many cases, to the student of general vertebrate physiology. The new edition is well indexed and illustrated and includes a pertinent bibliography after each chapter.



## ANGINES LYMPHO-MONOCYTTAIRES, AGRANULOCYTOSE, LEUCÉMIES LEUCOPÉNIQUES.

By Jean Sabrazès and René Saric. *Masson et Cie, Paris.* 40 francs.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; 363; 1935 (paper).

This is a detailed description of three distinct clinical syndromes: mononucleoses, agranulocytoses and aleukemic leukemias, which, however, have a number of signs and symptoms in common. Each of the three syndromes is considered in a separate section in which the authors discuss the history, symptomatology, clinical forms, hematology, anatomic lesions, bacteriologic and experimental investigations, therapy. In addition, throughout the text there are interspersed typical case

histories taken from the authors' own practice.

For a subject that is undergoing such rapid progress, the review of the more important world literature here found is really excellent. Special credit should be given to the attempt to coordinate into one system the viewpoints of the several investigators in this field.



THE WOMAN ASKS THE DOCTOR.

By Emil Novak. *The Williams and Wilkins Co., Baltimore.* \$1.50. 8 x 5½; x + 189; 1935.

This is an exceedingly careful and thoughtfully written book for lay consumption. Thirty years of gynecological practice have well fitted the author to write a book which will answer many of the questions which occur to a woman at some time during her life. The first nine chapters are devoted to different aspects of menstruation. Chapter ten is entitled "Woman as an Egg Producer" and discusses among other things the "safe period," in which the author has a considerable amount of belief. The last chapters discuss such things as common disorders of menstruation, sterility in women, and cancer.



CLINICAL PARASITOLOGY AND TROPICAL MEDICINE.

By Dámaso de Rivas, in collaboration with Carlos T. de Rivas. *Lea and Febiger, Philadelphia.* \$5.00. 9½ x 5½; 367; 1935.

A useful volume for the student and practitioner. Written primarily as a textbook, the authors' aim has been to present accepted facts concerning the modern conceptions of tropical and parasitic diseases from the standpoint of etiology, the complete life history of parasites, the pathology, symptomatology, diagnosis and treatment of these affections. For the sake of brevity theories and speculations have been eliminated. The volume is well illustrated and includes a list of references to the texts and articles drawn upon, and an index.

THE INFLUENCE OF CONCOMITANT ACTIVITY AND FATIGUE UPON CERTAIN FORMS OF RECIPROCAL HAND MOVEMENT AND ITS FUNDAMENTAL COMPONENTS. *Comparative Psychology Monographs, Vol. 11, No. 4, Serial No. 54.*

By David P. Boder. *Johns Hopkins Press, Baltimore.* \$1.75. 10 x 6½; 121; 1935 (paper).

The investigator was able to record four different components of the process of tapping with an extended index finger or tool. These components he lists as: "(1) The movement up, (2) the upper reversal, (3) the movement down, (4) and the bottom reversal." He discusses at length variability in the "tapping pattern," as to rate and form of the stops.



THE CONQUEST OF DEATH. *An Imminent Step in Evolution.*

By Annie C. Bill. *A. A. Beauchamp, Boston.* \$3.00. 7½ x 5½; 432; 1935.

The essential thesis of this prolix work is that, since death is not a natural phenomenon inherent to cell life, man can conquer it by somehow (not very clearly stated) obtaining a period of "organized conscious endeavor."



GESUNDES LEBEN.

By F. Külbs. *Georg Thieme, Leipzig.* 4.80 Marks. 8½ x 5½; 203; 1935.

The author endeavors to give a few simple rules of hygiene for the instruction and guidance of the layman. Diet, exercise, and rest are treated with most emphasis, and nothing new is pointed out. To the ordinary American, who is very hygiene conscious, the book will appear merely sensible and obvious, but for the European many current health fads are exploded.

LES IONOGRAMMES DE LA CONTRACTION MUSCULAIRE (*Technique d'enregistrement et résultats*). *Actualités Scientifiques et Industrielles, 245. Exposé de Biologie Générale en rapport avec la Cytologie, IV.*

By M. Dubuisson. *Hermann et Cie, Paris.*  
12 francs. 10 x 6½; 34; 1935 (paper).  
This is a description of methods of recording graphically the electric phenomena in muscular contractions. The resistance of ionized spaces of the muscle does not appear to change during contraction. However, the resistance of polarized interphases is modified. A short bibliography is provided.



*Krebs im Lichte biologischer und vergleichend anatomischer Forschung.* II. Band, 2. Heft: *Adenokrebs, Kystom, Scirrhus, Bindegewebe, Mesenchym, Sarcom, Odontom, Kieferkystom.*  
By Jos. Latschneider. *Franz Deuticke, Leipzig and Vienna.* 7 marks. 7½ x 5½; 197; 1935 (paper).

Earlier parts of this work have already been noticed in this REVIEW (Volume 9 Number 3, and Volume 10, Number 2). In this part cancers of the connective tissues, mesenchyme, and the jaw are discussed. The volume is equipped with index, bibliography and illustrations.



*INDIVIDUAL EXERCISES. Selected Exercises for Individual Conditions.*

By George T. Stafford, Harry B. DeCook and Joseph L. Picard. *A. S. Barnes and Co., New York.* \$1.00. 9 x 6; ix + 111; 1935 (paper).

This book emphasizes the importance of exercise to attain maximum health. One hundred exercises are described and illustrated. They are suggested in various combinations for fifteen types of physical defects.



*HEALTH AND EFFICIENCY HOLIDAY ANNUAL.*

*Published by Athletic Publications, Ltd., Link House, London.* 1 shilling. 11 x 8½; 63; 1935 (paper).

Directions for planning a holiday, nude or clothed, on a bicycle, in a caravan, at the seashore, in a boat, or camping.

*QUARTERLY BULLETIN OF THE HEALTH ORGANISATION. Volume IV, Nos. 1 and 2. Health Organisation, League of Nations, Geneva; World Peace Foundation, 8 West 40th St., New York.* Annual subscription \$2.50; separate issues 65 cents. 9½ x 6½; 192; 1935 (paper).



## BIOCHEMISTRY

*TRAITÉ DE CHIMIE ORGANIQUE. Tome I. Analyse Organique, Azéotropisme et Distillation, Etat Cristallin et Etat Colloïdal, Composé Défini et Corps Pur, Construction de L'Édifice Moléculaire; Association des Atomes, Chaînes Ouvertes et Chaînes Fermées. Groupements Fonctionnels. Représentation des Édifices Chimiques. Isomérisie. Nomenclature.*

By P. Bary, M. Delpine, Ch. Dufraisse, G. Dupont, V. Grignard, M. Lecat, R. Locquin, Ch. Mauguin, H. Pariselle, J. Timmermans. *Published under the direction of V. Grignard and Paul Baud. Masson et Cie, Paris.* 220 francs. 9½ x 6½; xix + 1149; 1935.

This is the first volume of a didactic and critical work on organic chemistry which will ultimately comprise 15 volumes. It is the first book of an encyclopaedic nature to be published in French in this field since that of Béhal and Valeur, now long out of print and out of date. Throughout this work the nomenclature of Geneva will be used as far as possible. The several chapters are by specialists in their field. A bibliography follows each chapter, and each volume will be equipped with its own indices—authors cited, substances by names and substances by formulæ.



*CLINICAL DIAGNOSIS BY LABORATORY METHODS. A Working Manual of Clinical Pathology. Eighth Edition, Thoroughly Revised.*  
By James C. Todd and Arthur H. Sanford. *W. B. Saunders Co., Philadelphia.* \$6.00. 9½ x 5½; 792; 1935.

This well-known text on clinical laboratory technique has been revised by the addition of a new chapter on clinical

chemistry; by the reorganization and extension of the material on blood chemistry; by the discussion of pathogenic organisms not discussed in earlier editions, and by the addition of 25 new illustrations. The chapter on clinical chemistry discusses methods for the determination of fibrinogen, cholesterol, sugar tolerance evaluations, blood salts and other such matters.

This edition has a workmanlike appearance and will undoubtedly retain and increase its present popularity.



L'ÉLECTROACTIVITÉ DANS LA CHIMIE DES CELLULES. *Actualités Scientifiques et Industrielles*, 244. *Exposés de Biophysique*, II. By René Wurmser. Hermann et Cie, Paris. 18 francs. 10 x 6½; 82; 1935 (paper).

A presentation of the methods and results of recent work on the electro-chemical equilibrium of cells and on the oxidation-reduction potentials of diastases. A chapter each is devoted to the application of the principle of Nernst and the electro-metric method for the determination of the constants of equilibrium. A bibliography of 96 titles is appended.



NATRIUMGEBREK BIJ RATTEN. (*Sodium Deficiency in Rats*.)

By P. Schoorl. N. V. Uitgevers-Maatschappij, Deventer. F. 2.50. 9½ x 6½; 90; 1934 (paper).

These experiments show the effects of sodium deficiency in rats. Since their intake of food and digestion is practically unchanged it is felt that the decrease in growth is a result of increased nitrogen metabolism. The sodium deficient rats showed greater activity and their body temperatures were subnormal.

## SEX

THE SEXUAL RELATIONS OF MANKIND.

By Paolo Mantegazza. Translated from the Latest Italian Edition, as Approved by

the Author, by Samuel Putnam. Edited with an Introduction by Victor Robinson. Eugenics Publishing Co., New York. \$3.00. 9½ x 6½; xxiv + 335; 1935.

Any realistic book on the sex life and practices of primitive peoples has a certain value and this one by Mantegazza is no exception. That it has proved generally interesting to its readers is attested by the fact that the book is now in its eleventh Italian edition and has been recently translated into English. The volume deals with such topics as the festivals of puberty; the sexual embrace and its forms; various types of sexual perversions; rites and customs associated with marriage, prostitution, monogamy, polygamy and polyandry, etc.

There are several criticisms which can be made of the work. In the first place, it is not as readable as it might be. Much of the text sounds simply like a log of isolated and uncorrelated observations, which detracts from its literary smoothness. Also most of the data presented are based on extremely old observations: most of the references cited date around 1850 to 1875. Lastly, there is an annotated appendix at the end of the book which does not seem to be accurately linked up with the specific cross-references in the text.



BIRTH CONTROL AND ITS OPPONENTS.

By Frank W. White. John Bale, Sons and Danielsson, London. 3s. 6d. net. 7½ x 4½; xi + 164; 1935.

In this little volume Mr. White makes a strong plea for birth control. He examines the populations of the past, how they have been regulated by wars, pestilence and famine, and the populations of the present, how they have grown because of modern hygiene, and may in the future increase enormously if wars are abolished. He argues that the outstanding benefits to be derived from an intelligent employment of birth control "will completely revolutionize the whole of human affairs, making life for the masses a fuller, higher and altogether better thing." Two chapters are devoted to the nature of the opposition to birth

control and the arguments put forth by the Church, war lords and a certain type of capitalist. Since the vast bulk of the well-to-do are themselves actively practicing birth control he finds that the opposition is really expending all its energies in an attempt to withhold the methods of birth control from the poor and unfortunate. The volume is without index. Lord Horder contributes a foreword.



#### GLÁNDULAS ENDOCRINAS Y PROSTITUCIÓN.

By J. J. Berastevide and S. Rosenblatt.  
"El Ateneo," Calle Córdoba 2099, Buenos Aires. 9 x 6½; 254; 1935 (paper).

The authors have obtained fairly complete personal histories of 110 prostitutes who were also subjected to a thorough physical examination including the usual tests of endocrine function. In the opinion of the authors, the findings indicate that in the majority of these women there occurs hyperactivity of the sexual glands and the pancreas and hypoactivity of the pituitary, adrenals and parathyroids. The thyroid is usually normal in function. It is to be noted that most of these women are illiterate or semi-literate, of poor families, etc. The general conclusion, cautiously advanced, is that for these women the social and economic factors merely act as a stimulus towards the realization of their endocrine constitution.



#### L'IMPUISSANCE SEXUELLE CHEZ L'HOMME. Étiologie. Diagnostic. Traitement.

By M. Palazzoli. Masson et Cie, Paris. 45 francs. 10 x 6½; vii + 284; 1935 (paper).

Male sexual impotence is here considered as a clinical entity and the author emphasizes its organic causes. The first part of this book fully describes the act of copulation, the anatomic structures involved and the probable physiologic reactions that take place. In the second part the author discusses the different forms of impotence and their presumed organic and psychic causes. The third part is on

therapy. Without doubt this is a valuable book for the clinician but it also deserves to be read by the human biologist, since the author makes apt comments on a number of sex problems.



#### LA FECONDITÀ LEGITTIMA DELLA DONNA SECONDO L'ETÀ.

By Giovanni Lasorsa. Antonio Milani, Padova. L. 15. 9½ x 7; vi + 81; 1934 (paper).

The author has calculated the age specific birth rates (number of children born to 1000 married women of each age group) for Sweden (1891, 1921), Australia (1911), Budapest (1891, 1895), Berlin (1891), Rome (1895), Trieste (1900), Milan (1931), Turin (1931), Venice (1931). For each of these groups, the distribution of the rates, in order according to increasing age of the mothers, is found to be well represented by a third order parabola. This volume presents the actual and calculated data.



#### SEX WORSHIP AND DISEASE (*Phallic Worship*). *A Scientific Treatise on Sex Worship and Its Influence on Religion and Symbolism, with Special Reference to Disease of the Sexual Organs.*

By Mason Daugherty. Mason Daugherty, 7909 Euclid Ave., Cleveland. \$3.50. 7 x 4½; 240; 1935.

This booklet contains a pot-pourri of odds and ends about sex matters culled from several well-known sources, including the Bible. It might appeal to adolescents.



#### BIOMETRY

##### THE RANGE OF HUMAN CAPACITIES.

By David Wechsler. The Williams & Wilkins Co., Baltimore. \$2.50. 8½ x 5½; ix + 159; 1935.

The author proposes that human variability be measured by the ratio: maximum/minimum and discusses its statistical and



biological significance. Though it seems strange that the proposed constant has not been used before, a superficial review of statistical literature confirms the author's assertion that his is the first publication in which it is mentioned. As a matter of record, it is well to recall that on April 27, 1935, at the sixth annual meeting of the American Association of Physical Anthropologists, Dr. Raymond Pearl read a paper entitled *Biometric Methods in Anthropometry*, in which he advocated the use of this same ratio, discussed its biological meaning, presented the results of application to about 700 series of measurements, and correlated these results with those obtained by the use of the coefficient of variation.

In the actual computation of this ratio the author uses as minimum and maximum respectively the second and 999th individual per thousand. The interval between the second and 999th is regarded by him as the range of normal variation. The author is of course free to use what limits seem more appropriate to him, but he goes further and attempts to give a rational justification of its use. This is unfortunate. Furthermore, he apparently does not foresee the case of J-shaped or other asymmetrical curves. The author has calculated this ratio for 89 series of measurements of human traits and finds that the values of this constant vary from 1.03 to 3.87. The frequency distribution of these ratios shows modes at the classes 1.20-1.29, 1.50-1.59, 2.00-2.09, and 2.50-2.59. The author believes that "all these modes may be looked upon as significant human constants. . . ." He is of the opinion that the value 2 is of special significance and discusses it at length. One can make a number of objections to such a statement. The principal objection is that this ratio, like all measures of variation, is affected by the scale of measurement. For example, the author finds this ratio = 1.03 for body temperature when measured in Fahrenheit degrees. If a centigrade scale had been used the ratio would have been different. Similarly for the blood pH this ratio is small because the pH is expressed in logarithms; a very different ratio would have been obtained if the antilog. were used. Since Pearl's

data showed values of 30 and above for certain traits, it is probable that as the author increases the number of series his views on the significance of the modal values will also alter.

This book contains a number of interesting observations on the subject of variation and some valuable data. However, with regard to this ratio the author has apparently allowed himself to be carried away by his own enthusiasm.



#### THE DESIGN OF EXPERIMENTS.

By R. A. Fisher. *Oliver and Boyd, Edinburgh.* 12s. 6d. net. 8 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; xi + 252; 1935.

The most effective use of the statistical methods expounded in Fisher's well known *Statistical Methods for Research Workers* depends upon a suitable design of the experiment to which the methods are to be applied. In consequence successive editions of that work have contained more and more detailed expositions of the technique of agricultural experimentation. Realizing, however, that the design of experiments is too important a subject for any incidental treatment to be adequate, Fisher has now written the present book, devoted to the study of experimental designs which have been successful in many fields of work and of the basic principles underlying them.

It is often stated in discussions of scientific methodology that only one essential factor at a time should be allowed to vary. As Fisher points out, this neglects the possible interactions of factors. In an agricultural experiment the yield of a crop for different amounts of nitrogen supplied in fertilizer may depend on the amount of phosphorus supplied. If the phosphorus ration in all the experimental plots is held constant there is no way of testing this possible interaction. On the other hand, if we hold the phosphorus ration constant within groups of plots but vary it from group to group, not only will the functional relation of yield to nitrogen and to phosphorus separately be determined with as great precision as if one factor alone had been tested, but any inter-

action between the two factors will be made plain. The book contains bibliographies and an index.



#### STATISTICAL PROCEDURES AND THEIR MATHEMATICAL BASES.

By Charles C. Peters and Walter R. Van Voorhis. *School of Education, Pennsylvania State College, State College.* \$1.50. 8½ x 5½; vii + 363; 1935.

The aim of this excellent textbook is to give the mathematical development of the standard statistical formulae in such a manner that persons who have studied only high school mathematics can follow it. The introductory chapter explains so much of calculus as is needed in the subsequent proofs, while the latter are given in such detail that the inexperienced student will not be confronted with an "it is obvious" which to him is by no means obvious. Although the intention of the authors is to show the derivation of the conventional formulae rather than to derive new ones, a few new methods are developed. Among these are tetrachoric and bi-serial correlations where only the two tails of one of the distributions are known. Exercises and references are given at the end of each chapter, and the appendices give tables of the normal probability integral and for use in tetrachoric correlation. The book will be found useful both as a text in mathematical statistics and as a reference book.



#### STATISTICAL METHOD IN EDUCATION.

By Charles W. Odell. *D. Appleton-Century Co., New York.* \$3.50. 7½ x 5½; xx + 457; 1935.

This book is designed to meet the statistical needs of those interested in the field of education by presenting the subject in a manner as non-mathematical as possible." The subjects treated are tabulation and classification, graphic representation, the normal and other frequency curves, averages, quartiles, percentiles and similar measures, measures of variability, correlation and regression of both

zero and higher orders, and the reliability of statistical constants. Besides numerous bibliographical footnotes, a general bibliography of four pages, tables of the normal probability curve and indexes are given.



#### PSYCHOLOGY AND BEHAVIOR

GROWTH: *A Study of Johnny and Jimmy.*

By Myrtle B. McGraw. *D. Appleton-Century Co., New York.* \$3.50. 9 x 5½; xxi + 319 + 20 plates and 5 folding graphs; 1935.

The much publicized investigation on the developmental behavior of a pair of twins is here reported in detail. As is known, one of the twins (Johnny) was, for a period of time since birth, stimulated to certain physical activities while the other (Jimmy) was kept more or less inactive for the same period and only at a later date given the training that his brother had received. The essential results are that for those "action-patterns [which] are, on the whole, indispensable to normal human functioning and stand as landmarks in the development of the human species" the effects of training were practically nil when considered in terms of time of onset and rate of progress. But for such activities as swimming, roller-skating, etc. Johnny developed more rapidly and showed greater proficiency than Jimmy. However, when towards the end of the experimental period (over 24 months) both children were presented simultaneously with new types of problems also involving motor functions, both reacted in practically the same manner.

In addition to the report of this unique experiment, which of course does not permit generalizations, the author discusses at great length and clearly, various aspects of the development of behavior-patterns.



#### ADULT INTERESTS.

By Edward L. Thorndike and the Staff of the Division of Psychology of the Institute of Educational Research of Teachers College, Columbia University. *The Macmillan Co.,*

New York. \$3.25. 7½ x 5½; ix + 265; 1935.

This book reports a part of the extensive and intensive study of the problems of adult education that has been going on under the author's direction for a number of years. Chapter V reports some interesting experiments leading to the following conclusions:

As the representative results described above show, the rate of learning does not suffer greatly even when what is learned is utterly valueless to the learner. Extrinsic interests are adequate to maintain learning when intrinsic interests are not available or require an undue expense of time, labor, or skill on the part of the teacher.

On the whole, we may conclude from the experiments that when certain unpalatable mental medicines need to be taken, too much time and pains should not be taken to disguise them. If a stretch of dull learning can be learned as it is in ten hours, it will usually not be profitable to spend five hours in making it so interesting that it can be learned in seven.

There are chapters on changes of intensity of interest with age, differences between young and old interests and attitudes, and interest and the curriculum of part-time adult education.



#### A DYNAMIC THEORY OF PERSONALITY. *Selected Papers.*

By Kurt Lewin. Translated by Donald K. Adams and Karl E. Zener. McGraw-Hill Book Co., New York. \$3.00. 9 x 5½; ix + 286; 1935.

For the most part the Gestalt school of psychologists have dealt with problems of perception and learning rather than with the more difficult, but none the less important, fields of will, emotion and character. Lewin, however, has extended the Gestalt viewpoint to the investigation of the latter subjects. In the first article of the present book he elaborates the idea that as physics developed from an Aristotelian viewpoint full of valuative concepts—e.g. circular orbits as the highest form of motion—and tending to identify the individual with the accidental to a Galileian viewpoint which rejects valuative concepts and regards the individual as well as the regular and uniform as being subject to law, so psychology is about to pass through an analogous development.

Other articles deal with the structure of the mind, environmental forces in child behavior and development, the psychological situation of reward and punishment, education for reality, substitute value, a dynamic theory of the feeble-minded, and a survey of the experimental investigations of his school. The book contains bibliographical footnotes and an index.



#### THE EVOLUTION OF MODERN PSYCHOLOGY.

By Richard Müller-Freienfels. Translated by W. Brian Wolfe. Yale University Press, New Haven. \$5.00. 9 x 6; xvi + 513; 1935.

Müller-Freienfels has written a first-rate history of the development and critical interpretation of practically every school of modern psychology (individual, social and racial) plus a few less authentic offshoots such as telepathy, palmistry and astrology. He not only traces their development one from another, but gives an unbiased evaluation of their contributions, and points out their differences, similarities, and shortcomings. The book is, it seems to us, one of the most adequate and stimulating of its kind, and due to its non-pedantic style is suitable for the intelligent layman as well as the psychologist and psychiatrist. It is indeed fortunate to have this book made available to English readers in so competent a translation as this one. A bibliography and author and subject indices are included.

#### PSYCHOLOGY OF LEARNING. *A Textbook in Educational Psychology.*

By Robert A. Davis. McGraw-Hill Book Co., New York. \$3.00. 8 x 5½; xii + 489; 1935.

A first rate text-book for an advanced course in educational psychology. The chief purpose of the book is to give students an opportunity to consider critically studies with somewhat divergent results as well as some of the many theories advanced on disputed facts. The important works and many of the more promising theories on the psychology of learning

processes are reviewed and critical suggestions offered. Many of the studies are presented in tabular and graphic form with the essence of each set forth "in a brief space in such a way as to enable the reader to obtain the trend of them all, if there is a trend, or to be sure that the whole question is unsettled because of the mélange of results." The volume is documented and contains an index of authors and of subjects.



#### CHILD PSYCHIATRY.

By Leo Kanner. Charles C Thomas, Springfield, Ill. \$6.00. 9 $\frac{3}{8}$  x 6 $\frac{1}{8}$ ; xviii + 527; 1935.

This book, with prefaces by Dr. Adolf Meyer and Dr. Edwards A. Park, is a thorough analysis of the difficulties of childhood. The author deals fully and sympathetically with the various mental disorders of children from the very young to the adolescent, and covers every subject from thumb sucking to sexual practices. His theories are amply illustrated by numbers of actual and interesting cases with which he has come in direct contact. An important book.



#### LA DÉMENCE.

By Raymond Mallet. Armand Colin, Paris. 10.50 francs (paper); 12 francs (cloth). 6 $\frac{1}{2}$  x 4 $\frac{1}{2}$ ; 176; 1935.

A short treatise on the clinical, anatomic, pathogenic and therapeutic aspects of the different types of mental disorder, with particular reference to newer developments in diagnosis and treatment. An attempt is made at classification of the various types by beginning and terminal stages. There is a short bibliography and an index of names.



#### DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

#### LA MATIÈRE.

By Georges Lakhovsky. Gaston Doin et Cie, Paris. 24 francs. 7 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; 232; 1934 (paper).

This book is about the *Universion*. "Universion" is a French portmanteau word, made up of *univers* and *ion*—as simple as that. But, ah, what it means! It is a non-material force which occupies inter-molecular space, and is, in the end, to be identified with God. Lakhovsky's view is that the density, mass, and radiation of each material body from stars to atoms are functions of the *compression* created by this body in the *universion*, and this *compression* provokes a perpetual dynamism which accounts for the motion of the bodies. [Reginald, the Office Boy, whose attitude towards sacred and spiritual matters regrettably gets less reverent as he grows older, says that he tried substituting God for universion in the preceding sentence according to directions, and got as a result a wonderful picture of Divine Borborygmus. He thinks that the author should introduce bicarbonate of soda somewhere into his cosmic system.]

What the good old universion can do for us may be illustrated by the following passage which appears in the chapter on Universion—Light—Heat.

One can then comprehend that a person born on our Earth fifty years ago and still living is multiplied to infinity on all those planets where his complex of radiations has gone to be materialized at different times. It is thus, for example, that a man sixty years of age, who at the end of his earthly life, can be born again at this moment on another earth seventy light years distant from our globe. And this can be repeated to infinity in space and time. Human life will therefore appear on different planets as a series of successive and eternal resonances.

In the light of the preceding, one should be able to give every appeasement to scholars who are confronted with unsurmountable difficulties in conciliating their scientific principles and religious scruples.

Thus the miracles reported by religion, particularly the dogma of the Immaculate Conception, can be explained as the result of the action of the materialization of a higher Being by the condensation of radiation emanating from the Universion-God on our Earth.



#### A HISTORY OF SCIENCE, TECHNOLOGY, AND PHILOSOPHY IN THE 16TH AND 17TH CEN- TURIES.

By A. Wolf, with the co-operation of F. Dannemann and A. Armitage. The Macmillan Co., New York. \$7.00. 9 $\frac{3}{4}$  x 6; xxvii + 692 + 68 plates; 1935.

This excellent history well fulfills its dual purpose of being of use both to the general reader and to the serious student. The description is in sufficient detail to enable the reader to understand what the various scientists were really doing. The author deals not only with astronomy, mathematics, mechanics, physics, meteorology, chemistry, geology, geography, the biological sciences, and medicine, but with technology, psychology, the social sciences, and philosophy. Over 300 well chosen illustrations add to the interest of the book. Bibliographic references are included in the text.

This is intended to be the first of three volumes, of which one will deal with the eighteenth and nineteenth centuries and one with ancient and medieval times. We wish Professor Wolf all success in the completion of a work which will be of great value to those interested in our cultural heritage.



THE ENDLESS QUEST. *Three Thousand Years of Science.*

By F. W. Westaway. Blackie and Son, Toronto and London. \$7.00 (Canada); 21 shillings (Great Britain). 8½ x 5½; xx + 1080 + 51 plates; 1934.

This book is as intriguing as its title from the first chapter on the "Geography of the Ancient World" to the last on "The Passing of Dogmatism." It is necessarily rather brief in some of its parts due to the wide scope of the whole, but the reader is given an absorbing moving picture of the history and development of science through the ages. Throughout the book stress is laid on the laboratory and field work of history in contrast to the theoretical and speculative. The material is presented in a critical fashion that draws the reader into valuing for himself the evidence by which the inferences are supported. Books for reference are listed at the end of each chapter, and there is an extensive subject index as well as a name index.

LA PENSÉE ET LE MOUVANT. *Essais et Conférences. Cinquième Edition.*

By Henri Bergson. Félix Alcan, Paris. 25 francs. 8½ x 5½; 324; 1934 (paper).

In the first two essays of this volume, which are hitherto unpublished, Bergson outlines the method which he believes is appropriate for the development of philosophy and repels the charge of anti-intellectualism and hostility to science which has often been made against him. Science and metaphysics, in his view, are coördinate; the former by the use of the intellect deals with matter, the latter by the use of intuition deals with mind. The other essays and lectures have as subjects the possible and the real, philosophical intuition, the perception of change, introduction to metaphysics, the philosophy of Claude Bernard, the pragmatism of William James, and the life and work of Ravaisson, the French philosopher and educator.



HANDBOOK OF TRAVEL. *Second Edition, Revised and Enlarged.*

Prepared for the Harvard Travellers Club; Edited by Geo. C. Shattuck. Harvard University Press, Cambridge, Mass. \$3.00. 6½ x 4½; viii + 510; 1935.

Much of this handbook is designed for the traveler in countries without benefit of Cook's or the American Express Company. The prospective explorer can find here useful information on planning a caravan or sledding expedition, packing a dromedary, dealing with native servants, etc. The traveler in less remote regions will be repaid for reading the chapters on automobiles, canoes, motor boats and sail boats. Besides this discussion of methods of travel, information is given on camping; photography; recording of geographical, geological, anthropological and meteorological observations; collecting of zoological and botanical specimens; and hygiene, medicine and surgery. Brief bibliographies are appended to many of the chapters and a detailed index is given. A useful book.

## THE WORK OF SCIENTISTS.

By Edith M. Patch and Harrison E. Howe.  
The Macmillan Company, New York. 76  
cents.  $7\frac{1}{2} \times 5\frac{3}{8}$ ; viii + 488; 1935.

This book deals with the sciences and their application to modern life. It should prove interesting and instructive to children of primary school age.

UNIVERSITY OF COLORADO STUDIES, Volume 22, Number 4. Containing following articles: *The Observance of Holidays and Vacations by the Lower Exchequer, 1327-1336*, by James F. Willard; *Contemporary Life in Two*

*Twelfth-Century Saints' Legends*, by Irene P. McKeehan; *Some Observations on the So-called "Plural Majesty" or Plural of Reverence*, by Edwin B. Place; *On Certain Adverbial and Semi-adverbial Uses of "bel," "beau" in Old French*, by Paul-Louis Faye; *Anglo-Latin Scholarship, 597-780*, by Jack D. A. Ogilvy; *Tacitus through the Centuries to the Age of Printing*, by Mary F. Tenney; *Bishops and Monastic Finance in Fourteenth-Century England*, by Harold E. Aikens; *Chancery and Exchequer Clerks serving as Attorneys, 1327-1336*, by Thomas W. Simons.

University of Colorado Press, Boulder.  
\$1.00.  $10 \times 6\frac{1}{4}$ ; 116; 1935 (paper).





# THE QUARTERLY REVIEW of BIOLOGY



## THE BLACK WIDOW SPIDER

By FRED E. D'AMOUR, FRANCES E. BECKER AND WALKER VAN RIPER  
*Research Laboratories, University of Denver*

### INTRODUCTION

THIS study was undertaken somewhat in the nature of a summer diversion. Our interest in the black widow spider was first aroused by the work of Blair (1) which received considerable publicity during the winter and spring of 1934. When it was found that these spiders were fairly numerous in and around Denver, and a search of the literature indicated that many points concerning their life history and the properties of their venom were not definitely established, a modest research program devoted to their study seemed to promise considerable enjoyment, even though the results might not have an exceedingly great scientific value. Since we could hardly hope to make a specialized study in any one particular field, we decided to explore all of them a little. In consequence, this paper gives findings covering various aspects of the problem. In the first part the appearance of the spider is described, and observations concerning its natural history recorded.

In the second, studies concerning the toxicity of the venom, its chemistry,

immunology, toxicology, and pathology are reported. Most of the experiments herein reported were carried out during the summer of 1934. However, delay in publication permits inclusion of certain observations and experiments conducted during 1935, especially relating to the production of sheep anti-serum. This work was carried out in cooperation with the E. R. Squibb & Sons Company. The total number of spiders collected has been about 6,500, and some 500 rats have been used.

The literature up to 1932 has been adequately reviewed by Bogen (2); reference to other important work will be made in the appropriate place.

### NATURAL HISTORY

Spiders have a life that is vivid and intense, though so unobtrusive that we usually do not see them, or at most pay little attention to them. Specialists find them fascinating as a group because of their anatomical peculiarities, their production of silk, and their habits of preparing snares for prey. Laymen are but little interested in spiders because their apparent economic value is negligible.



The average person is likely to have an active dislike, if any feeling at all, for spiders. This dislike is not based on justifiable fear. The effect of the bite of a spider has long been a question. The Tarantula, a small wolf spider of southern Europe, figured in early legends because of the music and extravagant bacchic display designed to incite the patient to the violent dancing which was thought to be the sole cure for its bite.

The only other type of spider that has gained a wide and infamous reputation is *Latrodectus*, a genus of the family Theridiidae. Stories of the deadly nature of the bites of these spiders are current among the peoples of all the regions of the world in which they occur. It is difficult to believe that there is no basis in fact for the similar beliefs that have grown up in such widely separated regions as Europe, America, Madagascar, New Zealand, Algeria, and the West Indies. Arachnologists of the old school were inclined to believe that the stories were based on mistaken evidence. Even today some maintain that the reports of the venomous qualities are greatly exaggerated. In the case of *Latrodectus*, incomplete observation gives conflicting evidence. There are authentic reports of bites of this genus of spider being followed by no harmful results. There are equally authentic reports of fatalities, or of more or less serious and disagreeable symptoms, followed by recovery.

The divergence of opinion in regard to the effect of the bite has a simple and reasonable explanation. All spiders have poison glands, which open near the tips of the fangs of the chelicerae. The contents of the poison sac are expelled by muscular action, undoubtedly voluntary on the part of the spider. A "bite", therefore, does not necessarily imply the injection of the venom, but might be

entirely harmless. The injection of varying amounts of venom would explain the gradations in the seriousness of the consequences. Nothing but carefully controlled laboratory experiments can give conclusive evidence in a question of this sort.

The fact that the spider has many common names indicates an enforced recognition. The natives of Madagascar know their two species as "Vancoho" and "Mena-vedi". The New Zealand species is the "Katipo". *Latrodectus* *13-gattatus* of southern Europe is known as the "Malmignatte". The common American species, *Latrodectus mactans*, was the "Pokomoo" of the Indians, who knew the potency of its venom for making poisoned arrows. Other common names for this spider are the "Black Widow", the "Hourglass", or "Shoebutton" spider.

The Standard Dictionary says that the derivation of *Latrodectus* is apparently from two Greek words meaning "pay received". Jaeger (Dictionary of Latin Combining Forms Used in Zoological Names) derives it from *latro*, Greek, a robber; and *dect(o)*, Greek, to bite, biting, a biter; hence, *Latrodectus*, a robber-biter. *Mactans* is a Latin word meaning "murderous".

#### Distribution

The most recent review of the distribution of the black widow which has come to our attention is that of Burt (3). This study, combined with that of Bogen, leaves only the following states from which the black widow has not been reported: Oregon, Minnesota, Iowa, Missouri, Wisconsin, Illinois and Vermont. It is almost certainly present in Oregon, in fact, very probably it will be found in every state of the Union. According to Phillips (4), Canadian records are available for the provinces of Alberta, British Columbia, Manitoba and Ontario, and

southward its range in the mainland extends at least to Peru. The species has also been reported from the West Indies.

### *Habitat*

The web of the black widow is an irregular structure, made of coarse, elastic, tough silk. There is usually a central nest or pocket about the size of one's finger to which the spider retreats when she is frightened, and to which she carries many of her meals. The web is evidently being constantly renewed and repaired, as the silk in an abandoned web is dull in appearance, brittle and weak and easily distinguished from the silk in an occupied web. The structure may be of no greater extent than the mouth of a gopher hole, or as much as a yard each way on the surface of a bank, probably being enlarged with the constant renovation. Once the widow has established her web, she is not likely to be found outside of it unless by accident or intent some superior force drives her out. When this happens she shows her discomfort and fear by timid and awkward actions. With the onset of cold weather, however, many reports have reached us of spiders crawling about on walls and floors of dwellings. Apparently the cold has driven them inside and they are hunting a more favorable winter residence.

The location of the web seems to be largely a matter of chance, though in our locality some favorite sites are permanent holes or fissures in a bank, such as the excavations made by swallows in a clay bank; in brick, rock, or trash piles; in sheds, garages, outbuildings and basements; under loose rocks and in eroded holes in granite; in tile roofs, etc. Webs and spiders have been found in abandoned birds' nests in the pine trees of the foothills. Recently we found the whole south side of a new country house in the

suburbs of Denver harboring young widows of this season in every possible retreat behind shutters, rain spouts, etc. Webs have been observed in the prickly pear cactus, where they spread about in the branches of the plant, with the central nests in the trash on the ground. In the summer of 1934, perhaps owing to the dryness, these spiders seem to have invaded the residential districts in unusually large numbers, and one of us actually found a mature black widow ensconced behind some books in the library. Reports have come to us of their being found commonly in box cars and a communication from fruit growers on the western slope of the Colorado Rockies stated that grapes were going to waste because pickers refused to work among the spider-infested vines. We have seen the black widow or had reports of her in all parts of Colorado. One was collected at an altitude of 8000 feet near Buffalo Park, the record altitude so far as our personal experience goes, and we collected specimens both in 1934 and 1935 at an altitude of about 7300 feet in Estes Park. Recently we have received from a trustworthy source a record of one taken near the village of Estes Park at an altitude of 8200 feet.

It is evident from the above statements that the spider recognizes few geographic barriers except extreme cold and is also easily satisfied with her local surroundings. At the same time, we have found certain particular locations very densely populated and it would appear that these are the most favorable in insuring survival. As stated, we have collected approximately 6500 spiders. By far the greatest number of these were captured in the foothills country between Denver and Colorado Springs. The hill sides are of disintegrating limestone, forming fissures and clefts in the cliff faces, and with many boulders on the gentler slopes. On the

south slopes of these hills and canyons, nearly every cleft and hole in the cliff has a web across its mouth, nearly every boulder a web along its lower margin. The insect life is not particularly abundant, but in such regions as this one can collect several hundred spiders within a few hours. It should be noted, however, that the size of the spider seems to be in direct proportion to the size of the rock and to collect large specimens one must have the fortitude to turn over large rocks.

The web serves as a snare for the prey on which the spider feeds—flies, beetles, grasshoppers, and the other insects that blunder into it. We have even observed a small mouse entangled and several times have seen the large Western cicada, which is nearly as big as a mouse, a victim. Usually whatever touches the web is securely caught almost at the first contact, and its struggles only tie it the more tightly. Large grasshoppers, however, can kick themselves free and require prompt and energetic measures on the part of the spider. She belongs to the family of "comb-footed" spiders which are distinguished by the presence on the tarsus of the fourth pair of legs of a distinct comb, consisting of a row of strong, curved, and toothed setae. The comb is used for flinging silk, in an almost liquid state, over the entangled prey. It is interesting to see the technique employed in subduing one of the larger grasshoppers, an animal considerably bigger and many times stronger than the spider. What she does is to hog-tie the powerful jumping legs of the victim and after submission is gained in this way she takes her time about administering the fatal bite.

#### *Hibernation*

In the vicinity of Denver we have been able to collect specimens in every month

of the year. The degree of activity shown by spiders collected in the winter months appears to depend on the temperature; if it is warm, individuals captured behave about as they do in summer; if it is cold, they are more or less torpid. They have been found in winter in all the common places and we have never observed the slightest evidence of special preparation against the cold—nothing in the way of additional web or better protection for the nest. Many of those found under rocks and in trash heaps appear to have made no webs of any kind. In December last year, after a heavy snow with cold nights, we picked up a specimen from the bottom of a pile of tumble-weeds, about as wet and cold a spot as one could imagine. Later, in an unheated room, where half a dozen recently collected spiders were exposed to a temperature of 10 degrees below zero in a sudden cold snap, all were frozen.

#### *Methods of Collecting*

*Latrodectus* is ready both by day and by night for any passing victim and at night is easily spotted with a flashlight. An easy method of collecting from holes in banks and similar places is to tie a beetle to a string eighteen inches or so long with the other end of the string attached to a stick of handy size. When the beetle is dropped into a web, if the spider is hungry, she will at once rush out to capture the struggling insect. Web and spider may then be struck down and the spider transferred by means of forceps to the collecting bottle. Sometimes one may pull out web and egg-sacs so that they dangle just outside the hole. After some time the female may frequently be caught outside in the act of rescuing her eggs and repairing the damage to the web. During the capture of the widow she almost always exhibits the cataleptic

reflex, "playing possum," a protective habit that is common to almost all kinds of spiders, and when picked up by a leg with the forceps she is likely to cast the leg, another protective device that is familiar to spider observers everywhere.

#### *Temperament*

The widow is generally found alone, since her fierce and predaceous habits cause her to kill any insect invader, or be killed. The "killer instinct" is apparent in the following description of a typical conflict observed in a web located in a well-lighted hole, about eye level, in a brick-yard bank. The occupant was a large female with two egg-sacs in the upper part of the web. She was hanging back down on one of the sacs—a characteristic position. A small mirror was used to shine light into the hole so that everything might be clearly seen. The observer placed another widow, previously collected, into the outer part of the web. There was no movement for a moment; then the alien oriented herself and moved a short distance into the web. The occupant countered by leaving the egg-sac and advancing a spider's length toward the interloper. Both advanced and stopped alternately until they approached each other in the center of the web. All their movements were deliberate and cautious. There was a moment of absolute stillness, then with a motion too quick for the eye, the occupant threw a shower of thick, sticky silk, which spurted from the spinnerets at the tip of the abdomen and was flung over the invader by a skillful manipulation of the hind legs. The victim was rapidly rolled over and over in a net until it was completely covered like a mummy. It was only then, when the risk was past and all secure, that the poison bite was administered.

Contests staged in the laboratory established the fact that a bite upon another spider causes paralysis immediately, but does not necessarily produce death. Victims removed from the web after they were helpless and all prepared for the victor to begin feeding, were found to recover their powers of motion after several hours, and to be apparently normal the next day. In contrast to the fierce nature of the spider toward others of her kind, is the extreme timidity which she exhibits toward unnatural disturbances of her web, such as might be caused by a collector. At the first molestation of the web, she retreats with incredible speed into the central nest, and does not venture out again for hours. We have never seen the slightest attempt at defense, to say nothing of aggression, on her part under such circumstances.

#### *Reproduction*

In mid-summer nearly every web of *Latrodectus* that is found is occupied by a mature female guarding her eggs, and one hardly ever sees a male. As fall approaches the mature females decline in number and the collector everywhere meets females recently matured or in late stages, and males of the same ages in almost equal numbers. By late summer males and females are to be found living in the same webs, few of which now contain egg-sacs. Apparently the mature females met in summer are the immatures of the previous fall. After the cycle of maternal functions is completed, they die out, which explains the scarcity of adult females as fall approaches. Ordinarily the life cycle appears to be a little over a year, but this probably varies according to environmental factors.

We have witnessed the actual mating on three different occasions. The first was between a female which only the day

before had completed her final molt, and a male which, because of his size and light color, was thought to have several stages yet to go to maturity. As the mating of spiders has not often been observed, and that of the black widow in particular has not been recorded before, so far as we know, we shall describe the occurrence in some detail.

On the morning of August 11th one of us (W. V. R.) observed a web across the mouth of a large hole in a bank of the Platte River. The web was found to contain three males and a large female. No egg-sacs were present. During the course of the day courtship between one of the males (the largest of the three, although his coloring was not that of a mature male) was observed. At long intervals he slowly approached the female, waving his forelegs and, when near, he tentatively stroked her. She responded by exhibiting great anger, shaking the web and lunging at her suitor, who made off rapidly. She made no effort to pursue him; he, in his turn, occasionally chased the other males away, in a mild, half-hearted manner. Once he rested for twenty minutes with the tip of one foreleg touching the tip of hers. Suddenly she jumped at him and seized him and could easily have destroyed him had her hostility been real.

The observer returned that night, thinking that with creatures reputed to be nocturnal, events might progress more rapidly then. Fabre states that the only mating he ever witnessed took place at night. However, the flashlight seemed to disturb the female who kept out of sight most of the time.

On returning the next morning, it was found that one of the males was missing. The chief characters, however, were still engaged in courtship, the female seeming more willing to permit the advances of

the male, although too great a degree of intimacy was still resented. This continued throughout the day. It being no longer possible to continue the observations in situ, the specimens were captured and placed in bottles in the laboratory. The female was left alone for several days to become accustomed to her new home. One morning it was found that she had eaten a beetle and also undergone a molt. This last may be of significance if it be true that sexual maturity is not reached until the final molt. The male was now introduced. Within a few hours he recommenced his advances and this time she appeared willing to permit them. She hung motionless in her web, abdomen up, the male excitedly crawling all over her. There followed periods of quiet, the male occasionally coming to rest close to the female. At such times it was noted that his abdomen vibrated with great rapidity. The vibrations are necessarily transmitted to the female by means of the web and perhaps serve to excite the female sexually or notify her of the presence of a lover. Finally, after repeated maneuvers of this sort, the male again approached the female and came to rest upon her abdomen, his head at the level of her epigynum, the tips of their abdomens even. The female remained motionless and apparently indifferent. Fecundation then took place, the male inserting first the intromittent organs of the right pedipalp, his body shifted somewhat to the left. Contact was continued for fifteen minutes. He then retreated momentarily, then returned and, with body shifted to the right, introduced the organ of the left pedipalp for a period of ten minutes. He then retreated, wiping the pedipalpi with his forelegs. The female followed him. He ventured a parting caress only to be struck at viciously.

For the next few days the pair was

closely observed. Traditionally the female should kill the male immediately or at least very soon after mating. They were well supplied with grasshoppers and beetles, of which both partook. Finally, after ten days, the lifeless body of the male was found hanging in the web. She certainly may have killed him, although there are reasons for doubt. First of all, he had shown himself throughout equally as agile, perhaps more so than she, and had had no difficulty avoiding her previously. Furthermore, the other male taken from the same web and kept alone was found dead a day later and a third male, collected elsewhere, died within the week. All the males that we have attempted to keep in captivity have lasted but a few months at best and this fact, coupled with the observation that males become very rare in the middle of the summer and are only plentiful in spring and fall, leads us to think that the life cycle of the male is considerably shorter than that of the female. Thus it seems quite possible that the widow may be a relict, not as a result of her own criminal propensities, but from natural causes alone.

The mating just described took place on August 18. The female was kept in a quart specimen jar and fed on grasshoppers and beetles, later on meal worms, then was transferred to a milk bottle containing an ordinary fruit fly culture and stoppered with a wad of cotton, this being an easy and successful way of wintering these spiders. In the spring she was put back in the specimen jar and fed meal worms and angle worms. Not until July 12 did she produce her egg-sac. This produced spiderlings in the normal way within the next month, and not long after she was dead. She was being fed on angle worms at this time and, as a number of other deaths occurred within a short period, we

came to the conclusion that these worms may not be a suitable diet. In contrast to this female, which carried the sperm to fertilize her eggs just one month short of a year, another which was observed to mate on June 11, 1935, produced an egg-sac on July 6. We have also had a female which produced three egg-sacs from none of which spiderlings emerged, only to be followed by a fourth with a normal emergence. The third mating, which occurred on August 14, 1935, involved a female which had occupied a web in the garage of a friend for the entire summer and a male which appeared suddenly only a day before the mating occurred. Very careful notes of the proceedings were kept by Mrs. F. W. Miller, to whom our thanks are due. The mating required nearly three hours, the details being much as described above. The sequel, however, was quite different. Upon completion the partners withdrew some distance, with, however, no signs of hostility, and occupied the same position the last time they were inspected that evening, at about 11:00 p.m. The next morning, however, to our great astonishment, we found the female dead, and the male feeding upon her. There was no sign of any accident, the web had not been disturbed. Whether he had killed her or not we do not know. But she was dead, he was alive and was eating her, the ancient tradition to the contrary notwithstanding.

#### *Development*

Many of our females produced from one to four egg-sacs in captivity. The process probably generally takes place at night, but was several times observed in the laboratory during the day. We found an average of 143 eggs in ten sacs, the maximum being 210. The eggs are whitish, smaller than the head of a common pin,

and covered with a sticky substance. The egg-sac mentioned above as being produced on July 6 was started at 8:40 in the morning. This female was confined in a square glass case about eight inches high and six across. She had previously settled on one of the upper corners for her nest which was merely a roughly funnel-shaped thickening of the web. Working, as always, from below, she first spun a shallow disk about a half-inch in diameter. Against this she pumped up a sticky, yellowish mass of eggs, pausing to rest from time to time. At 9:10 she was spinning a blanket around the eggs. We quote from our notes:

Two or three threads coming from spinnerets. She touches fabric with spinnerets, then draws away and handles threads with hind legs (these have the "combs"), then turns a little and does it again, making a very loose cottony felt all around ball of eggs. Color, white. That of egg mass, yellow. She is not disturbed by being moved. The egg mass can be seen in the center through the wall of felting. Egg ball about  $\frac{3}{8}$  inch in diameter. Felting  $\frac{1}{4}$  inch thick. Now 9:20. She is going over the surface, touches with spinnerets, then another spot close by. Not using legs to handle silk. The beat is 2 per second. This is evidently making outer coat. It is more yellowish than felt, but not as yellow as mass of eggs. She does not use her hind legs at all in this process. Just tap, tap, tap with spinnerets. Makes a fine fabric that quickly gets opaque. At 9:55 it is finished.

In nature the egg-sac is held in the web by stay lines, but may be moved with considerable facility. When the web is disturbed the spider quickly hauls the sac back as far as possible out of danger. When the sun is shining and nothing threatens, the sac is hung near the mouth of the web. Temperature and humidity are possible factors influencing the time of emergence, which is ordinarily from two to three weeks. Hatching from the eggs apparently may take place within a few days, but the young do not emerge for a varying length of time. From the fact that the magnifying glass shows

casts in the debris of the emptied egg-sac, it appears that the young make their first molt before escaping. Considering the minute size of the prisoners and the toughness of their confining walls, the problem of escaping must be a serious one. However, two or three pin-holes are eventually made in the sac and the spiderlings swarm out.

We have not succeeded in inducing the young to feed except upon each other, which may be their habit in nature. We doubt, however, that cannibalism begins while the spiderlings are still confined in the egg-sac. Many empty egg-sacs have been examined in our search for parasites and in the sac from which a normal emergence has occurred we usually find only casts and egg membranes, rarely a dead spiderling. Three egg-sacs produced at intervals by the same female were allowed to hatch in a single container. The older and stronger fed on the younger and upon each other till at the end of the summer only three, all females, had survived to approach maturity.

According to Lawson (5), eight molts take place before maturity, the ninth instar representing the adult stage. Food supply and environmental factors influence the time between molts, which is usually from 9 to 18 days. Under favorable conditions full development requires 2 to 3 months, sometimes longer.

#### *Appearance*

Progressively through the instars the specimens show changes in pattern and color. The characteristic markings are really beautiful. At all stages in both male and female the telltale hourglass may be identified on the ventral side of the abdomen, though it varies much in color. Lawson gives a detailed account of the appearance of the female in each instar. As we observed it, the basic color of the

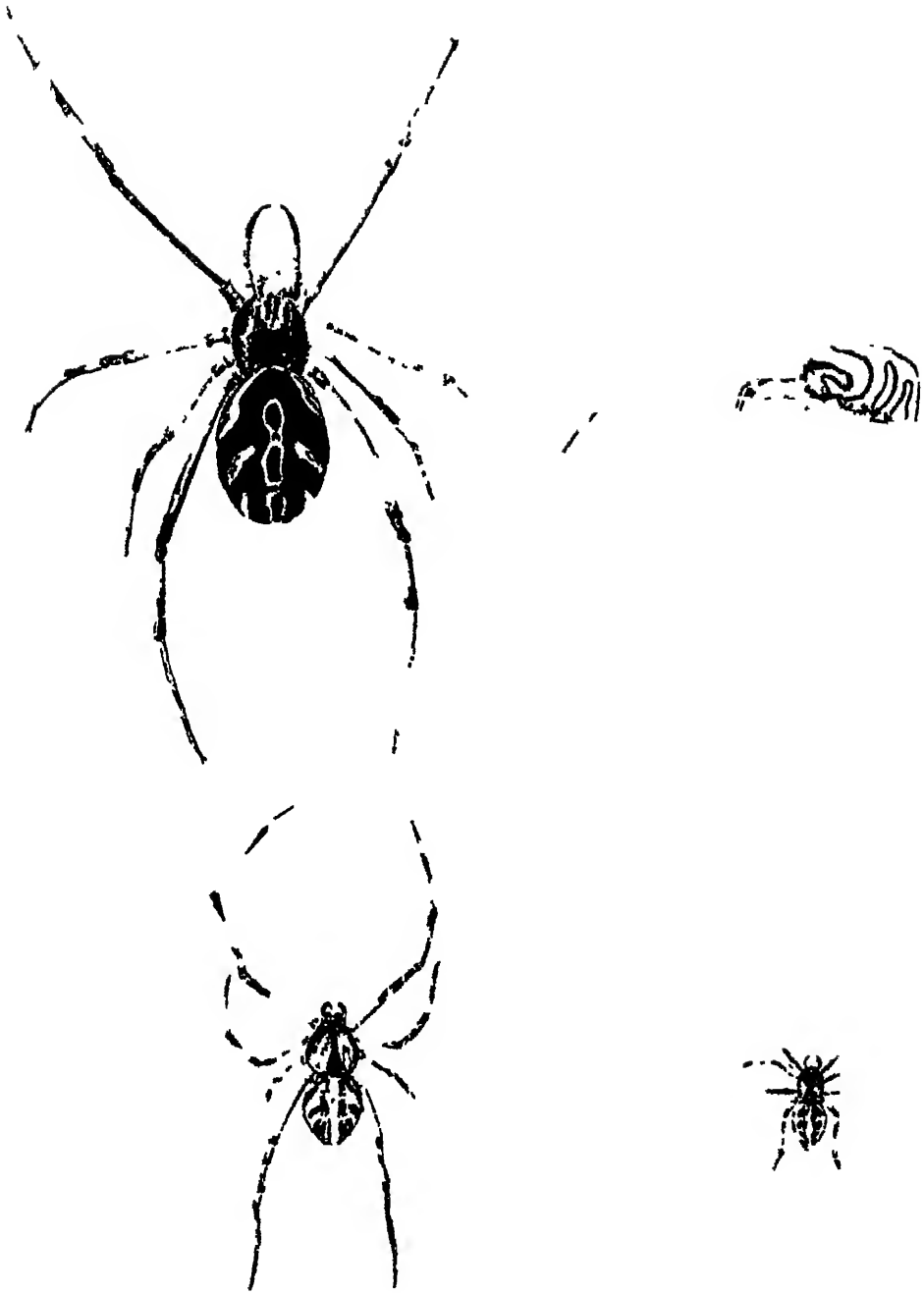


FIG. 1. FOUR STAGES IN THE DEVELOPMENT OF THE FEMALE

About two molt intervals. The largest is about two molts removed from maturity, the smallest is the spider from the egg sac.  $\times 6$



newly emerged spider is an olive drab, with the abdomen marked liberally above and below, with a dead white. Gradually as the molts proceed the basic color darkens, the legs are often banded with dark and light brown, the white areas decrease, the hourglass becomes more prominent, bands or spots of color, progressing from faint pink to orange, red, or yellow, appear along with the

of the abdomen. Both color and pattern are, however, subject to variations. The eight slender black legs cover a spread of as much as two inches in large specimens. See Figs 1 and 2.

The adult male has white stripes on the sides of the abdomen and a conspicuous orange dorsal stripe. It bears considerable resemblance to the immature female at certain stages. The male is



Female with egg sac X3

FIG 2. MATURE FEMALE IN CHARACTERISTIC POSITION GUARDING EGG SAC X3

white markings on the back. These latter markings generally disappear entirely with the last molt. The length of the fore tibia is used as the most reliable index to the developmental stage.

The adult female is a shiny jet black with the body proper about 1 to 1½ cm long. Body weight and size of the abdomen vary with the state of nutrition and the egg producing cycle. Generally the body is entirely black except for the orange-red hourglass on the ventral side

about one-fourth the size of the female, and has a slender rather than spherical abdomen. See Fig 3. The chief distinction between the two sexes is in the structure of the last joint of the pedipalps. These, the second of the two pairs of head appendages, are situated on each side of the mouth and are more or less leg-like in appearance. The female *Latrodectus* has the tarsus of the pedipalp ending in a single claw, as is true of the females of many genera. During the third instar of

the male the pedipalps show signs of enlargement, which progresses during the fourth and fifth instars. In the final molt complex intromittent organs are produced

cate web which the male spins. This fluid is then taken up by the specialized genital appendage of the palpus, by which it is transferred to the female at mating.

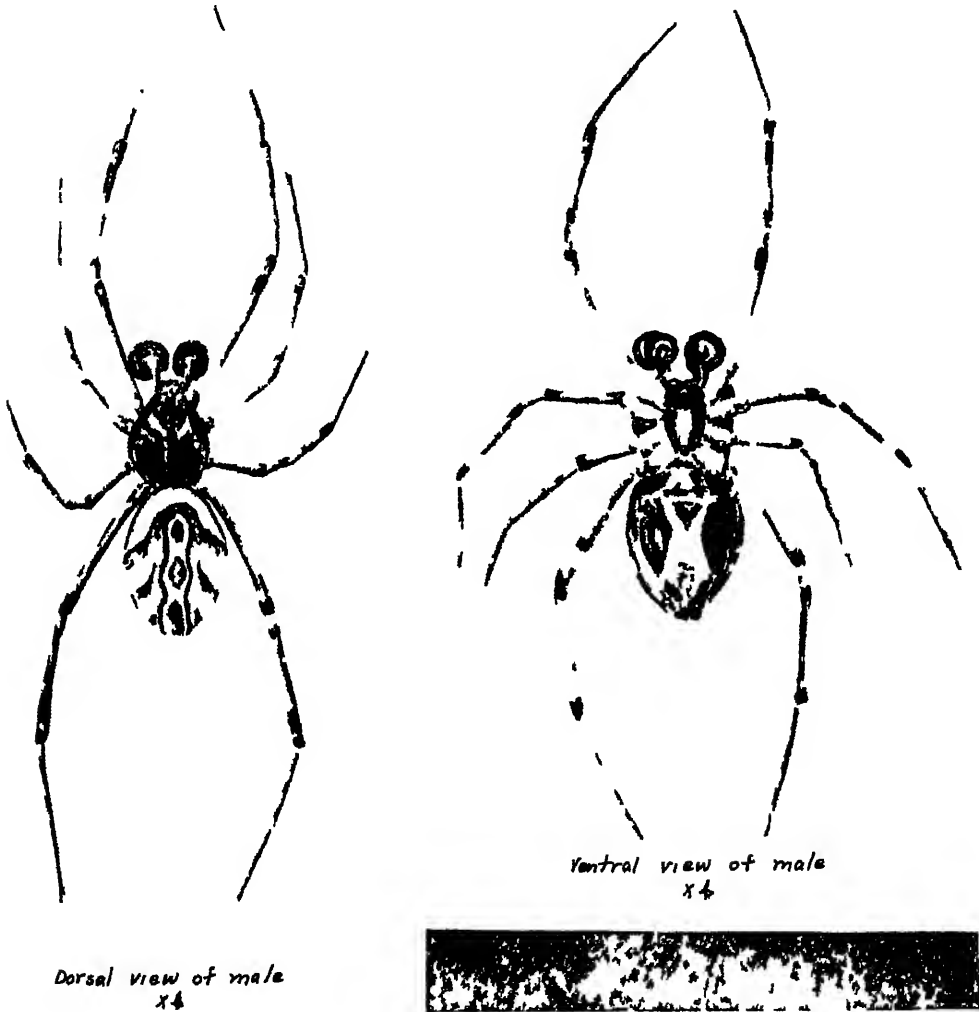


FIG 3 MALE PROBABLY MATURE, AT LEAST WAS CAPABLE OF FERTILIZATION  
Left—dorsal view Right—ventral view X 6

as bulblike structures on the ends of the pedipalps. They have no direct connection with either testes or vasa deferentia. The seminal fluid produced in the gonads of the abdomen is deposited upon a deli-

The cephalothorax of the adult female seems to vary in proportion to the general size of the animal and the length of the appendages. It is somewhat shield-shaped, with four shallow acetabula on

each side to receive the coxae of the legs. See Fig. 4. The dorsal anterior angle composes the median ocular area, on which are located the eyes in two rows of four each. Beneath the eyes and

of insects. They are situated in front of and above the mouth. Invariably they are made up of two joints, the proximal parturion or tige, and the distal unguis or fang. The parturion is stout and conical

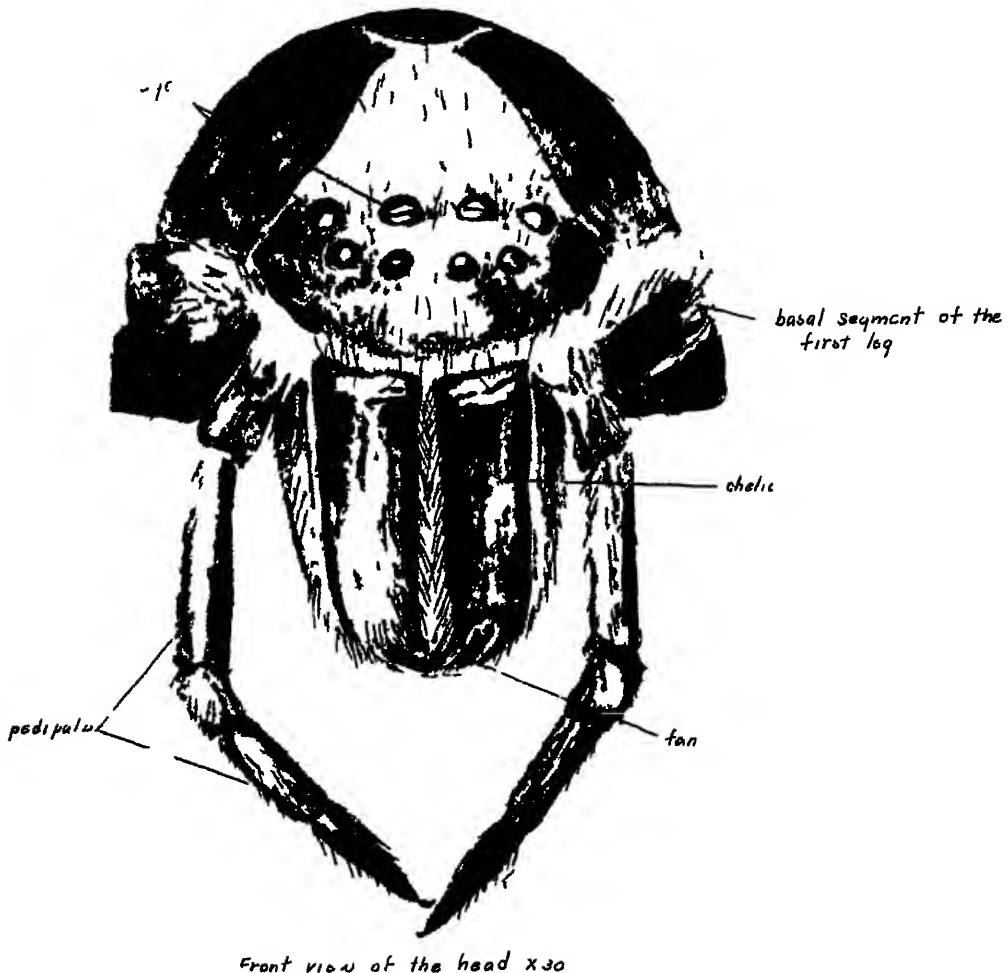


FIG. 4. DIAGRAMMATIC, ANTERIOR VIEW OF HEAD, SHOWING CHELICERAE AND FANGS OF MATURE FEMALE

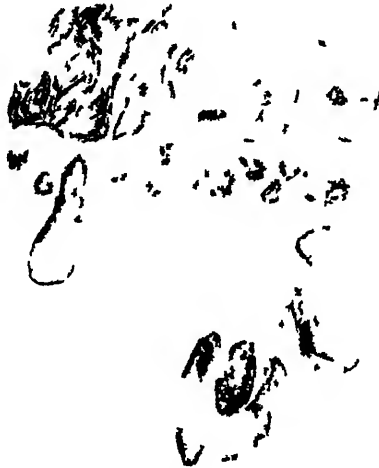
separating them from the first pair of appendages is a sclerite called the clypeus. The first appendages, or chelicerae, are homologous with the second antennae of crustaceans, and not with the mandibles

and well provided with stiff hairs. The unguis is a reddish brown, sickle-shaped claw of hard chitin. The chelicerae are articulated so that their principal motion is lateral with the two fangs directed

toward each other in action. The mouth is fitted for the taking of liquid food only. When the victim has been sucked dry, the hard parts are discarded. On the top of the cephalothorax just behind the ocular area is a smooth triangle set off by shallow grooves. Beneath this triangle and the ocular area lie the pair of poison sacs. Slender ducts lead through the hollow chelicerae and fangs to a mesial aperture close to the tip of the claw. It was found that the glands could easily be

be columnar and arranged in a single row with the nuclei toward the bases of the cells. See Fig 5. The cytological processes involved in the production of venom have not been worked out.

The poison glands of the male are in the same location as in the female, and of the same general appearance, but proportionately smaller. The male does kill small insects for food, but whether or not by the use of poison could not be ascertained.



*Portion of a cross section of a poison gland*

FIG 5. HISTOLOGIC SECTION OF VENOM GLAND

The masses represent secretion precipitated by fixing agent. Hematoxylin and eosin stain.

removed by a procedure described in detail later.

The glands are white, often curved, sacs, varying from 1 to 2.5 mm in length, and generally about 1 mm thick. The weight varies from 1.5 to 2 mg. The wall is surprisingly tough. The outer wall of the sac is made up of strong muscle fibers. Beneath the muscle layer is a thin sheath of connective tissue, supporting the secretory cells which project into the lumen of the gland. They appear to

Spiders show two definite tropisms. When they are young they are negatively geotropic, tending to climb upwards, at all stages they are negatively helio-tropic, tending to move away from the light. The geotropism of the young provides a means of dispersal. Once the maiden flight has been effected and dispersal accomplished, the spiders no longer exhibit the tropism. The following ob-

servations on the dispersal of the spiderlings were made by us.

A glass tube about an inch and a quarter in diameter and three feet long, enclosing a piece of bamboo of the same length wound with raffia, was closed with cloth at both ends after a newly made egg-sac had been placed inside on the bottom cloth. The whole contrivance was then set upright in a retort stand. The bamboo inside the glass tube would furnish the spiderlings something to climb on should they have the instinct to do so after emergence from the sac. About four weeks after the spinning of the sac, there were two little swarms of fifty or sixty spiderlings each at the base of the tube near the sac. During the day they all climbed their artificial tree and swarmed at the top of the tube. The next morning the apparatus was carried out into the country, the top cover removed, and the length of the artificial tree increased by a three-foot stick. Immediately about fifteen of the little spiders detached themselves from the swarm and intently climbed to the very tip of the new stick. The sun was shining and a little breeze blowing from the south. Suddenly a tiny mite was snapping about in space eighteen inches or two feet from the stick. It was a spiderling waving in the breeze at the end of a gossamer drag-line which it had spun as it was blown from its moorings. Then the spider was observed to be working its way back along the line, not drawing in the line but leaving it out, possibly doubling it. The adventurer reached his dock again, leaving the silken thread flapping in the breeze. Suddenly the line broke at its base, or was cut by the spiderling behind him, and he sailed away into space too rapidly for the eye to follow the course very far. This happened again and again, till of the

original fifteen adventurers only two or three remained. This explains the disappearance of the young spiders from the maternal web so soon after emergence, and explains also their being found later in life in curious places to which chance blew them on their initial flight.

When the young spider ends its voyage, we must imagine that it seeks the first hole or crack available as shelter. Here it spins a web not unlike that of the mother, but on a small scale, catches its prey in the same way, and if circumstances are propitious, sets up a permanent establishment.

#### *Enemies*

In spite of the fact that the poison of the widow is deadly to all small animals, she has a number of natural enemies. We have observed the vireo feeding the spider to her nestlings and pigeons and chickens may eat it with impunity, the latter with apparent relish. Field mice and related mammals probably take the spider when they find her, since we have never observed one under a rock that shelters rodents. Possibly some of the hunting spiders can overcome the widow, although in laboratory observation she has always prevailed over any other spider put in with her.

Newspaper items from time to time report discoveries of what we judge to be parasitic wasps and ichneumon flies designed to exterminate the black widow. Our observations indicate that she, when full-grown, can handle any wasp that might attack her directly. We have found, in the debris of the spider's web, in the empty egg-sacs and in various other similar places the active and omnivorous larvae of one of the Dermestid beetles, the common museum pests. Whether these grubs are only scavengers cleaning up the waste from the spider's table, or

are also capable of destroying the living eggs, we have not been able to determine as yet. But we suspect that both are true.

There can be no question, however, but that the blue mud dauber (*Chalybion cyaneum*, Klug) is a predator on the black widow. We have collected many mud dauber nests and have frequently found immature black widows stored as food for the larvae. Recently Irving and Hinman (6) have published similar findings. In Lamar, Colorado, where black widows have been extremely prevalent the past two years, residents have told us that the mud daubers seem unusually scarce. It may be that in nature the mud dauber is one of the chief factors in holding the black widow in check.

#### EXPERIMENTAL

##### *Studies on Toxicity*

The first problem was to study the toxicity of the venom and to develop a reliable means of assay. Most experimental studies previously reported fall under two heads as far as the source of the material used is concerned. Some workers have proceeded by placing the spider upon a shaved area of the animal used and pinching it with forceps until it bit. Others have used the macerated heads of the spiders as their experimental material. Early in our work we tried both methods, but soon learned that they were unreliable and that consistent results could not be obtained. If one employs the first technic, he encounters several factors which are difficult or impossible to control. The actual amount of venom introduced will obviously be dependent upon the size of the spider, its past history, (that is, how long since it last made use of its poison apparatus and the speed of regeneration of the poison), and upon the

degree of anger aroused by the pinching. As will be shown later, even under conditions which one might suppose would excite the greatest degree of anger, that is, after victory in mortal combat with another spider, the glands still contain a considerable amount of venom. It seems likely that the glands are under some degree of volitional control and the amount ejected will depend upon the degree of irritation of the spider. This is supported by the experience of Baerg (7)

TABLE 1

WEIGHT OF RAT	SPIDER	RESULTS
164 280	Large "	No symptoms. Comatose all afternoon and night, breathing shallow, hind legs paralyzed. Recovered.
308	Small	Symptoms much like above, in addition, foreleg paralyzed, large swollen area at site of bite. Recovered.
65	Average	Severe paralysis in all legs. Could not use legs, could be slid across table. Breathing became difficult, died after 48 hours.
73 80	" "	No symptoms. Slight paralysis, recovered.

who speaks of spiders which bit readily and caused severe symptoms while others attacked only under extreme provocation.

As for the second method, that of using macerated heads as a source of material, if a sufficiently large number of spiders is used, the size and past history factors are averaged and, of course, the question of degree of irritation does not enter. However, anyone who has ever dissected out the venom glands will have noted their toughness and elasticity. Macerating the heads, even though the operation

is carried out thoroughly, will certainly fail to crush all glands. An unknown number will escape maceration and will then be discarded with the debris. The following tables illustrate the above points. Table 1 gives the results of actual biting experiments. In these trials spiders were used which had been kept in the laboratory three days and had not been fed during that period. These were placed upon shaved areas of the rat's abdomen and excited to bite by being pinched with forceps. The results are seen to be very inconsistent.

In Table 2 the results of two experiments are shown in which macerated heads were used, 40 heads being used in each batch.

TABLE 1

BATCH	NO. OF RATS INJECTED	AMOUNT INJECTED	PER CENT DEAD
1	10	Equiv. 2 spiders	70
1	10	" 1 spider	10
2	10	" 2 spiders	0
2	10	" 1 spider	0

The wide variation in effect no doubt indicates failure to crush and extract all glands.

Comparison of these results with the toxicity curve for venom obtained later indicates that even in the more active preparation a large number of glands must have escaped extraction.

In view of the inconsistent results shown above we adopted the following procedure as a routine method in the preparation of all venom used in the succeeding experiments. No fewer than 20 spiders, in some cases as many as 80 spiders were used in the preparation of each batch of material and in this way individual differences were averaged. The spiders were placed under light chloroform anesthesia, the abdomen clipped off and the cephalo-

thorax and legs imbedded in molten paraffin on a microscope slide. Solidification of the paraffin held the spider in a firm mounting. Under the dissecting microscope the skin of the head above the eyes was clipped off; the venom glands were then clearly visible and could be removed with fine forceps. The glands were then placed in physiological salt solution and carefully pulled apart and thoroughly macerated. The glandular debris was transferred to fresh saline, again macerated and washed and discarded. The washings were added to the original solution.

Young rats, fifty to sixty grams in weight, were chosen as test animals, first, because of their availability in this laboratory and second, because preliminary experiments showed that they were quite susceptible. A relatively small amount of venom would cause death and an adequate amount would produce a chain of symptoms which was a very definite and constant one.

*The Toxicity Curve.* The work of Trevan (8) on biologic assays in general and the work of Coward and Burn (9) and ourselves (10) on the assay of estrin preparations has clearly indicated the necessity of using large numbers of animals in the assay of biologic preparations in order to overcome the individual variation which exists between animals of the same species, weight and age. In order to establish the toxicity of spider venom we therefore injected varying amounts into groups of ten rats per dose. Fig. 6 shows the results obtained, with the amount of venom indicated both in fractional parts per spider and in absolute weight.

As will be noted, the average lethal dose, that is, the amount of venom which will kill fifty per cent of the rats, is one-fourth the venom contained in the glands of one spider, or .032 mg. This is the

amount meant when the term "Average Lethal Dose" or "Equivalent of one-fourth spider" is used in describing subsequent experiments.

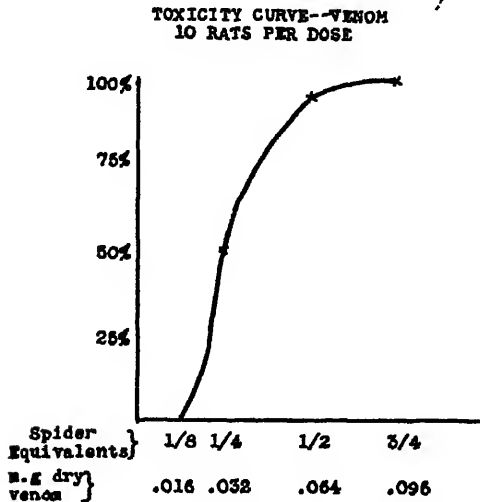


FIG. 6

use of the method which would require the least expenditure of venom, and having used this method in obtaining the toxicity curve continued with it in further experiments so that the results would be comparable.

*Weight of Rats.* The weight of the rat is an important factor in the amount of venom necessary to obtain a required result. For reasons given, we used immature rats weighing between 50 and 60 grams. Litters in prospect promised an adequate supply of rats of this size throughout the summer months. No extensive experiment was carried out to discover the ratio of venom to body weight; however, Table 4 gives the data on the few trials which were made.

*Type of Spider.* The spiders used throughout in the work reported elsewhere in this paper were mature females as indicated by the absence of any mark-

TABLE 3

TYPE OF INJECTION	NO. OF RATS	AMOUNT INJECTED	PER CENT DEAD	MAX. LIFE
Subcutaneous	5	Equiv. $\frac{1}{4}$ spider	0	—
"	5	" $\frac{1}{4}$ "	60	36 hours
"	5	" $\frac{1}{2}$ "	100	24 "
Intraperitoneal	10	" $\frac{1}{4}$ "	50	12 "
"	10	" $\frac{1}{2}$ "	90	8 "
"	10	" $\frac{1}{2}$ "	100	8 "

*Mode of Injection.* In obtaining the above toxicity curve, as well as in practically all of the later work, intraperitoneal injections were given. A preliminary study, the results of which are shown below, indicated this type of injection to be preferable inasmuch as the amount of venom necessary to cause death was somewhat less and also the length of time before death occurred was shorter when intraperitoneal injections were given. As we did not know in advance how plentiful the spiders would be, we naturally made

TABLE 4

NUMBER OF RATS	WEIGHT	AMOUNT INJECTED	PER CENT KILLED
10	50-60 gm.	Equiv. $\frac{1}{4}$ spider	90
4	100-150 "	" $\frac{1}{4}$ "	50
12	200-250 "	" $\frac{1}{2}$ "	33
8	200-250 "	" 1 spiders	100

ings on the dorsal surface. See Plates. However, it seemed desirable to investigate the toxicity of immature females and of males as well. For this purpose glands



from both groups were obtained in the usual way and injected. The results are given in Table 5.

These results indicate that the difference in toxicity is qualitative as well as quantitative.

*Toxicity of Baby Spiders.* As stated in the section devoted to natural history, the eggs hatch within the egg-sac and there the spiderlings undergo their first

venom glands would not be crushed in this process and the toxicity indicated in Table 6 resides in the tissue fluids of the spiders and possibly in unabsorbed egg material.

The results obtained later in the study of egg toxicity as compared with Table 6 show a much higher toxicity residing in the eggs. Apparently this material has been almost completely utilized by the

TABLE 5

TYPE OF SPIDER	NO. OF RATS	AMOUNT INJECTED	RESULTS
Immature Females	3	Equiv. $\frac{1}{2}$ spider	No symptoms
" "	3	" $\frac{1}{2}$ "	" "
" "	3	" 1 "	" "
" "	2	" $1\frac{1}{2}$ "	" "
" "	3	" 3 "	Sick, but recovered
" "	2	" 6 "	Very sick, recovered
Mature Males	1	" 12 "	Practically no symptoms
Mature Females	10	" $\frac{1}{2}$ "	50 per cent killed

Average Length of Venom Glands, Mature Females.....	1.75 mm.
" " " " " Immature Females.....	.75 mm.
" " " " " Mature Males.....	.75 mm.

TABLE 6

NUMBER OF RATS	AMOUNT INJECTED	RESULTS
5	Equiv. 1 spider	Slight paralysis, recovered
2	" $2\frac{1}{2}$ "	" " "
2	" 5 "	Severe paralysis, recovered
2	" 10 "	One died, other very sick, recovered

molt. It seemed interesting to compare the toxicity of the baby spiders with the eggs from which they came, therefore spiders 7 to 10 days after their emergence from the egg-sac were studied, as it was thought that much of the material from the egg would by that time have been utilized. Since it was impossible to dissect out the glands, the spiders were macerated in saline, the debris filtered off, washed in fresh saline and the washings added. Undoubtedly many of the

time the young spiders reach the age of one week.

*Degree of Exhaustion following Biting.* As previously mentioned, other workers have studied the toxic effects of the venom by causing spiders to bite their victims. Among others, Baerg (7) describes experiments done upon rats in which the first bite resulted in severe symptoms, a subsequent bite in less severe symptoms and the third in no symptoms whatever, from which he concludes that immunization

had occurred. As will be shown later, immunization develops much more slowly than these results would lead one to believe. In experiments done upon himself, Baerg obtained almost opposite results, the first bite causing only local pain, whereas the second was followed by a very serious and painful chain of symptoms.

We tested the question of the degree of exhaustion of venom in biting by placing the spiders under conditions where one would expect them to bite their hardest and to inject the maximum amount of venom. These spiders are notoriously

hour. It should also be stated that, where the spider was biting for the second time, the victim usually recovered. No experiments were carried out to determine the length of time necessary for regeneration of venom.

*Potency of Venom in Terms of Weight.* The poison glands were removed from twenty spiders and dried in air for twelve hours. They were then weighed. Following thorough maceration in distilled water the glandular debris was dried and weighed. The difference between the two weights is taken to represent the dry weight of the venom. This is not entirely

TABLE 7

	NUMBER OF RATS	AMOUNT INJECTED	RESULTS
Experiment 1	1	Equiv. 1 spider	Died
" 1	2	" $\frac{1}{2}$ "	Sick, recovered
" 2	1	" 1 "	Died
" 2	2	" $\frac{1}{2}$ "	Sick, recovered

cannibalistic. It is a well known fact and one which we have observed repeatedly, that when two mature females, especially if one is attending an egg-sac, are placed in one container, they will fight furiously until one or the other has been bitten and killed. We placed spiders together under these conditions; in the first experiment the victor of one match was matched with another victor; in the second, spiders were used which had only bitten once. The results are shown in Table 7.

The spiders in experiment 1 had bitten others twice within a half-hour before being killed, those in experiment 2 had bitten others once within a half-hour before being killed. These results show that the glands still contain a considerable amount of venom—at least one-fourth the total amount—even after the spider has used them twice within the previous half-

TABLE 8

Dry weight of glands from 20 spiders....	4.0 mg.
Dry weight of debris.....	1.48 mg.
Dry weight of venom.....	2.52 mg.
Dry weight of venom per spider.....	.126 mg.
Dry weight per A.L.D.....	.031 mg.

correct, since unavoidably some glandular elements were lost in maceration. The figure obtained errs, therefore on the side of assigning a somewhat lower potency to the venom than is actually the case. Table 8 shows the results.

These results indicate that on the basis of weight the venom of the black widow is extremely potent. In man, the spider bite results fatally in about five per cent of all cases (Bogen, 2). The rattlesnake is said to kill in from 15 to 25 per cent; the actual amount of venom introduced is, however, much greater in the case of the snake. Experimentally, Calmette found

that .2 mg. of cobra venom will kill a guinea pig, and Noguchi states that 5 mg. of rattlesnake venom will kill a 350-gram guinea pig in 24 hours. The following comparison of the potency of black widow with rattlesnake venom was made. Two specimens of the common prairie rattlesnake, (*Crotalus albicans*, Say) were collected, one a male three feet long with 8 rattles and the other a female two and one-half feet long with 6 rattles. The venom was obtained by pressing upon the glands, then dissecting them out and

TABLE 8a

NUMBER OF RATS	AMOUNT INJECTED	PER CENT KILLED
10	.75 mg.	0
10	1.0	90
10	1.5	100

spiders. Nine mature females were received which resembled our local spiders in every way but were somewhat smaller. The venom was obtained in the usual manner. The results are given in Table 9.

This seems to show a higher degree of potency for the local spiders. However, our assay was made on spiders collected during July; the Californians were collected in October, so a seasonal variation may be indicated.

*Toxicity Studies on Eggs.* A large amount of work has been done upon the hemolytic principle or arachnolysin of eggs, particularly by Levy (11). This poisonous material is found in the tissue fluids of all spiders, and reaches its highest concentration in their eggs. It appears to be fairly well established that the nature of this substance differs both in its chemistry

TABLE 9

	NO. OF RATS	AMOUNT INJECTED	PER CENT KILLED
Colorado spiders	10	Equiv. $\frac{1}{2}$ spider	50
" "	10	" $\frac{1}{2}$ "	90
" "	10	" $\frac{1}{2}$ "	100
California spiders	8	" $\frac{1}{2}$ "	25
" "	6	" $\frac{1}{2}$ "	33
" "	4	" 1 "	75

washing with distilled water and evaporating to dryness. 32 mg. of dried venom were obtained from the large snake and 20 mg. from the small. The venoms were pooled and assayed. The results are given in Table 8a.

As .064 mg. of spider venom killed 90 per cent of injected rats, it appears to be about 15 times as potent on a dry weight basis.

*Comparison of Colorado and California Spiders.* Through the kindness of Doctor Emil Bogen, of Olive View, California, we were able to compare the toxicity of spiders from that region with Colorado

and its effects from the venom. Since we intended to do some work on this question, particularly cross-immunization experiments, it seemed desirable to prepare a toxicity curve for eggs as well. This curve is shown in Fig. 7.

The dry weight of the egg poison was determined by macerating a weighed and counted sample of eggs, obtained from 10 different egg-sacs, in distilled water. The poisonous principle is apparently either a globulin or associated with globulins, as it is insoluble in distilled water but is soluble in dilute salt solutions. The solution was allowed to stand overnight

in the refrigerator and was then filtered. Upon drying, the precipitate is pale yellow and flaky in texture. The averages of several experiments, in which samples

brown house spider was made and indicated a much higher degree of toxicity resident in the black widow eggs. In both cases eggs were taken from ten different sacs and pooled. The results are shown in Table II.

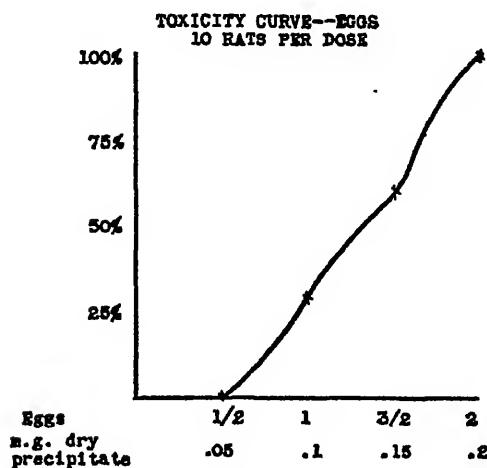


FIG. 7

*Keeping Qualities of the Venom and Eggs.* Various zoologists and popular writers on the black widow make mention of the fact that certain aboriginal tribes make use of both the venom and of the poison contained in the eggs to tip their arrows. Also it may become important in the gathering of venom for experimental purposes and in the preparation of serum, to know whether desiccation is resisted. On the third of July ten spider glands were macerated in a dry evaporating dish, covered with gauze and set aside at room temperature until August 23rd, when saline was added, the venom dissolved and

TABLE 10

MATERIAL INJECTED	NO. OF RATS	EQUIVALENT OF DRY MATERIAL	RESULTS
Fresh eggs	10	.1 mg.	30 per cent killed
" "	10	.15	60 " " "
" "	10	.2	100 " " "
Dried Ppt.	4	.1	0 " " "
" "	4	.25	50 " " "
" "	4	.5	100 " " "

were taken from 5 to 10 different egg-sacs, show that 1,000 eggs weigh 640 mg., and yield 100 mg. of dried precipitate. It should be pointed out that the figures in the above graph indicating dry weight were not obtained by actual injection of dried material, but were obtained by calculation. The actual injection of dried material shows a considerable loss of potency as a result of chemical manipulation or as a result of drying. This point is illustrated in Table 10.

A comparison of the toxicity of black widow eggs with the eggs of the common

TABLE 11

SOURCE OF EGGS	NUMBER OF RATS	NUMBER OF EGGS INJECTED	PER CENT KILLED
Black Widow		1	30
" "		2	100
Common Brown		3	
" "		7 1/2	0
" "		15	100

assayed. Forty eggs were handled in a similar fashion. Table 12 shows the results of the assay. These results indicate that there is little, if any, loss in

potency as a result of drying for a period of 7 weeks.

Venom dissolved in saline and allowed to stand at room temperature without preservatives for the same length of time had lost all potency. We did not study the effect of preservatives over long periods of time, but did determine that solutions made up either in 10% glycerin or in 1:1000 merthiolate did not lose potency when stored for a period of one week.

### Chemistry

*Chemistry of Egg Poison.* The very thorough work of Levy (11) on arachnolysins has elucidated many points of interest in regard to these substances. He, and others, believe them to be elaborated by

egg solution made acid (.1%) with HCl or alkaline with NaOH (.1%) removed nothing.

Exp. 2. Macerations of eggs in distilled water gave a solution in which a considerable amount of white material remained suspended. This was permitted to stand cold overnight, the precipitate was filtered off and washed. The precipitate was soluble in dilute salt solutions and in dilute acid or base. The following protein tests were strongly positive: Biuret, Millons, Adamkiewicz, and Hopkins-Cole. Assay of this material showed it to be toxic, although not as toxic as the original eggs, on the basis of dry weight. The filtrate and washings were combined and evaporated to a small volume. Pro-

TABLE 12.

MATERIAL	NUMBER OF RATS	AMOUNT INJECTED	RESULTS
Venom	2	Equiv. of 1 spider	All killed
"	4	" " $\frac{1}{2}$ "	" "
Eggs	2	" " 4 eggs	" "
"	4	" " 2 "	" "

all spiders, and present in all tissue fluids, reaching their highest concentration in the eggs and legs, and there is considerable evidence supporting the view that this poison is not identical with the venom. Our studies were directed mainly to this question which we attempted to solve by cross-immunization experiments. Some observations concerning the chemistry were made, however, and are reported here.

Exp. 1. A weighed quantity of the eggs were macerated in saline solution. This solution was neutral to litmus. Thorough extraction with ether yielded, in the ether fraction, a small amount (less than 1%) of a yellow oil, which, emulsified in water and injected, was shown to be inert. Subsequent ether extractions of the

tein tests gave a weakly positive Biuret and Millon test. The assay resulted negatively in the amounts used. The results are shown in Table 13.

From the above data it may be assumed that the toxic material found in the eggs is neither a lipoid nor an alkaloid, but is probably a globulin or associated with globulins.

*Chemistry of Venoms.* When venom glands are macerated in distilled water, a cloudy, opalescent solution is formed which is neutral to litmus. Standing in the cold causes a small amount of white precipitate to settle out. This precipitate is toxic, but accounts for only a small portion of the total toxicity. The precipitate gives the usual tests for protein and is soluble in dilute salt solutions. It

is our belief that it represents a globulin similar to, if not identical with that found in the eggs and is a contamination from the macerated glands rather than being the venom itself.

We proceeded, then, on the assumption that the venom is present in the distilled water filtrate. Ether extracts from neutral, acid, and alkaline solutions yielded extremely small amounts of residue which were inert. This would appear to rule out lipoids and alkaloids. The filtrate gives positive Biuret, Millon, Adamkiewicz,

the baths was evaporated to a small volume. This step was controlled by adding venom to equivalent amounts of water and evaporating for the same length of time. (Control 2.) The products were then assayed. The results are given in Table 14.

This experiment was repeated twice with the same result. The concentrated dialysates gave doubtful or negative Biuret tests, other protein tests were negative.

Since the venom is thus shown to be non-dialysable and associated with pro-

TABLE 13

MATERIAL	NO. OF RATS	AMOUNT INJECTED	RESULTS
Ether Extract (Yellow Oil)	2	Equiv. of 10 eggs	No effect
" " " "	2	" " 5 "	" "
Precipitate	4	" " 2½ "	50% killed
" "	4	" " 5 "	100% "
Conc'd. Filtrate	2	" " 15 "	No effect
" "	2	" " 7½ "	" "

TABLE 14

MATERIAL	NO. OF RATS	AMOUNT INJECTED	RESULTS
Control Solution 1	3	Equiv. of ½ spider	All died
" " 2	3	" " ½ "	" "
Non Dialysable Residue	8	" " ½ "	87% "
Concentrated Dialysate	4	" " 2 "	No symptoms

and Hopkins-Cole tests for protein, but might contain toxic non-protein constituents as well. We, therefore, next attempted to separate proteins from non-proteins by dialysis.

Collodion bags were prepared and tested to retain Congo Red. Two cc. of venom solution was placed in each bag and the bag suspended in 400 cc. of distilled water. The water was stirred frequently and changed each 24 hours, dialysis continuing for 72 hours. Control samples of venom in glass ampoules were placed in the same baths. (Control 1.) The water from

tein, our next efforts were directed toward separating the protein from any non-protein, non-dialysable substances which might be present. A great many spiders and much work were expended in these attempts, which, however, all resulted in failure, due to the extreme lability of the venom, probably indicating it to be protein which is easily denatured. Only two of the many experiments will be described, one in which the precipitating agent was sodium tungstate, the other methyl alcohol. In addition to these, precipitation with ethyl alcohol, ammo-

nium sulfate, lead acetate, and tannic acid was attempted.

Exp. 1. The venom glands of 60 spiders were macerated in 100 cc. distilled water and the solution allowed to stand over night. A small amount of white precipitate settled out which was filtered and washed. The precipitate was dissolved in saline. This is solution V-1. A portion of the filtrate was assayed as a control; this is solution V-2. To 5 cc. of the filtrate was added  $\frac{1}{2}$  cc. of 1% Na tungstate solution plus 3 cc. N/12  $H_2SO_4$ . A white precipitate formed, which was

It will be noted that the protein precipitate, (V-3), in large doses, was toxic, but that much of the potency has been lost. The loss, we believe, can be attributed to the action of the sulfuric acid, as Solution V-5 showed no toxicity whatever. This experiment was repeated three times, there was some variation in the toxicity of the original precipitate (V-1) and of the tungstic acid precipitate (V-3), in the latter case depending upon the length of time it was left in contact with the sulfuric acid. In every case, however, addition of dilute sulfuric acid to the

TABLE 15

MATERIAL INJECTED	NO OF RATS	AMOUNT INJECTED	RESULTS
V-1	4	Equiv. of $2\frac{1}{2}$ spiders	2 died, 2 sick but recovered
V-1	2	" " $1\frac{1}{2}$ "	Sick but recovered
V-2	2	" " 1 "	Died
V-2	2	" " $\frac{1}{2}$ "	Died
V-3	5	" " 2 "	2 died, 3 recovered
V-3	4	" " 1 "	Slightly paralyzed but recovered
V-3	4	" " $\frac{1}{2}$ "	No symptoms
V-4	3	" " 2 "	No effect
V-4	4	" " 1 "	" "
V-4	3	" " $\frac{1}{2}$ "	" "
V-5	3	" " 2 "	" "
V-5	3	" " 1 "	" "
V-5	2	" " $\frac{1}{2}$ "	" "

filtered off, washed and then shaken up with 2 cc. 5%  $CaCl_2$  to break up the protein tungstate. This was assayed as solution V-3. The filtrate from V-3 was neutralized with  $Na_2CO_3$  and assayed as V-4. To control the effect of the addition of acid, a portion of the original filtrate (V-2) had added to it 3 cc. of N/12  $H_2SO_4$ . It was allowed to stand the same length of time (approximately 5 minutes) as was required for the tungstic acid precipitate to form and be filtered, and was then neutralized with  $Na_2CO_3$ . This is V-5. The results are shown in Table 15.

original venom, for a period of 5 minutes or longer, destroyed the toxicity. This point will be stressed later. Exp. 2. Szu (12) has recently reported upon the ability of methyl alcohol to precipitate proteins without causing denaturation, providing the length of time allowed for precipitation was not too great, 4 hours being permissible in some cases. An attempt to precipitate with methyl alcohol is next described.

The venom glands from 40 spiders were dissected out and macerated in 10 cc. distilled water. One cc. was assayed as a control. This is M-1. To 4 cc. of the

remainder, 100 cc. of absolute methyl alcohol was added, and the solution, with frequent shaking, left in the refrigerator for 3 hours. A white precipitate formed which was centrifuged off, washed with methyl alcohol, quickly dried, and dissolved in saline. This is M-2. Four cc. of the remainder was treated in the same way, but only left standing for 1 hour. This is M-3.

The filtrates from M-2 and M-3 were evaporated to a small volume. These are M-4 and M-5 respectively. Finally, 1 cc. of the original venom was added to dis-

They showed no respiratory involvement whatever, the lachrymal glands were not affected, nor was there a discharge of bloody serum from the nostrils. Recovery from the paralysis occurred within 3 to 4 hours. So greatly did they differ from the controls and also from the picture presented by rats given sub-lethal doses of the straight venom that we are inclined to believe that there are two factors present, one of which, the more lethal, is destroyed or denatured by the alcohol, while the other, paralytic, factor is not affected. This seems the more

TABLE 16

MATERIAL INJECTED	NO. OF RATS	AMOUNT INJECTED	RESULTS
M-1	2	Equiv. of 1 spider	Died
M-1	2	" " $\frac{1}{2}$ "	"
M-2	2	" " 2 "	Paralytic symptoms, recovered
M-2	2	" " 1 "	" " "
M-3	2	" " 2 "	" " "
M-3	2	" " 1 "	" " "
M-4	2	" " 2 "	No symptoms whatever
M-4	2	" " 1 "	" " "
M-5	2	" " 2 "	" " "
M-5	2	" " 1 "	" " "
M-6	2	" " 1 "	Died
M-6	2	" " $\frac{1}{2}$ "	1 died, 1 recovered

tilled water and evaporated for the same length of time as the filtrates M-4 and M-5 in order to control the possible destruction by evaporation. This control is M-6. The results are given in Table 16.

The animals receiving solutions M-2 and M-3 (that is, the protein precipitates) gave a peculiar reaction. Paralysis of the legs set in very promptly and was just as severe as in the animals given straight venom. However, they showed none of the depression which venom poisoned rats invariably show; on the contrary, they tended to remain in motion, dragging themselves around as best they could, even trying to climb the side of the cage.

likely as there was no difference in the behavior of groups M-2 and M-3, in spite of the fact that the former solution had been subjected to the action of the alcohol for three hours instead of only one. In other words, time did not seem to cause a progressive destruction of a simple toxic principle. This experiment was performed twice with entirely concordant results.

Experiments performed to study the action of the digestive enzymes produced further evidence of the extreme lability of the venom. As will be described later, studies of the action when venom was given orally showed it to be harmless.



We, therefore, subjected the venom to the action of pancreatin and pepsin.

The venom glands from 40 spiders were macerated in 10 cc. distilled water and one-half used for each determination. One cc. was used as control. This was C-1.

**Pancreatin Digestion.** A 2% solution of pancreatin and a .5% solution of sodium carbonate were prepared and the

The results of assay are shown in Table 17.

**Peptic Digestion.** A 2% pepsin and a 1/10% hydrochloric acid solution were prepared, the following mixtures made up, and incubated at 37° for six hours.

1 cc. venom plus 1 cc. pepsin solution plus 1 cc. HCl solution = Pep. I  
1 cc. venom plus 1 cc. HCl plus 1 cc. distilled water = Pep. II

TABLE 17

MATERIAL INJECTED	NO. OF RATS	AMOUNT INJECTED	RESULTS
C-1	2	Equiv. of 1 spider	All died
C-1	2	" " $\frac{1}{2}$ "	" "
Panc. I	2	" " 1 "	No effect
Panc. I	2	" " $\frac{1}{2}$ "	" "
Panc. II	2	" " 1 "	" "
Panc. II	2	" " $\frac{1}{2}$ "	" "
C-2	2	" " 1 "	All died
C-2	2	" " $\frac{1}{2}$ "	Both very sick but recovered
C-3	2	1 cc.	No effect
C-3	2	$\frac{1}{2}$ "	" "

TABLE 18

MATERIAL INJECTED	NO. OF RATS	AMOUNT INJECTED	RESULTS
Pep. I	2	Equiv. of 1 spider	No effect
Pep. I	2	" " $\frac{1}{2}$ "	" "
Pep. II	2	" " 1 "	" "
Pep. II	2	" " $\frac{1}{2}$ "	" "
C-4	2	" " 1 "	All died
C-4	2	" " $\frac{1}{2}$ "	" "
C-5	2	1 cc.	No effect
C-5	2	$\frac{1}{2}$ "	" "

following solutions made up and incubated at 37° for six hours.

1 cc. venom plus 1 cc. pancreatin solution plus 1 cc. sodium carbonate solution = Panc. I

1 cc. venom plus 1 cc. sodium carbonate plus 1 cc. distilled water = Panc. II

1 cc. venom plus 2 cc. distilled water = C-2

1 cc. pancreatin solution plus 1 cc. sodium carbonate plus 1 cc. distilled water = C-3

1 cc. venom plus 2 cc. distilled water = C-4

1 cc. pepsin solution plus 1 cc. HCl solution plus 1 cc. distilled water = C-5

The results of the assay are given in Table 18.

While both pepsin and pancreatin incubation destroy the toxicity, the important point brought out in the above experiments is that incubation for 6 hours merely in dilute acid or base also destroys the toxicity. This is in agreement with

the point made in precipitation studies with sodium tungstate where addition of the sulfuric acid alone resulted in destruction and emphasizes the great lability of the venom and the ease with which it is denatured.

*Destruction by Heat.* No systematic studies were made of the degree of temperature and length of time of exposure necessary to destroy the venom. Two samples of venom were tested, one after being heated to boiling for five minutes, the other after heating to 75° for twenty minutes. In both cases the toxicity had been completely destroyed. As was noted above, heating to 37° for six hours did not destroy the toxicity.

no symptoms whatever, cannot be accepted for the reasons given earlier in the paper. We have several times permitted a spider to bite a rat without effect, the reason being that the spider was either not sufficiently irritated or had too recently exhausted her venom.

Early in June we set aside 26 rats for immunization; 10 were mature (average about 250 grams) and 16 immature, the latter representing the survivors of the toxicity curve determination. The mature animals were given  $\frac{1}{2}$  spider twice weekly for three weeks and  $\frac{1}{3}$  spider twice weekly for two weeks. The immatures were given  $\frac{1}{3}$  spider twice weekly for three weeks and then  $\frac{1}{2}$  spider twice

TABLE 19

NO. OF RATS	TYPES OF RATS	WEIGHT	AMOUNT INJECTED	RESULTS
10	Imm'd. Adults	200-250	Equiv. of 1 spider	All very sick but recovered
6	Control "	200-250	" " 1 "	" " " 1 died
16	Imm'd. Immatures	100-150	" " 1 "	" " " 6 "
4	Control "	100-150	" " 1 "	" " " 2 "

### Immunology

A considerable amount of research has been done in the study of the immunological aspects of this problem, notably by South American workers. The most conclusive evidence of anti-venin production was reported by Troise (13) who injected three rabbits with 14 injections each of dry venom over a period of 37 days and found, in the most favorable case, that .05 to .1 cc. of serum would neutralize, in vitro, 1 mg. of venom. He apparently did not study the protective action of serum when injected separately, nor the question of how long a time could be permitted to elapse between the venom and serum injections.

The work of Baerg (7) in which he caused spiders to bite rats, and found that the first bite caused severe symptoms, the second bite less severe, and the third

per week for two weeks. It was thought that by this time immunization had been effected and all animals were given the equivalent of one spider each. (The immature rats at this time weighed from 130 to 150 grams.) The results are given in Table 19.

These findings indicate that little, if any immunization had occurred and that, for the rat at least, immunization is a very slow process.

The survivors of the previously injected groups were then injected for another 5 weeks period. In the mature animals the dose was  $\frac{1}{2}$  spider every other day for the first 3 weeks, then  $\frac{1}{3}$  spider every other day for the following 2 weeks. The immatures were given  $\frac{1}{3}$  spider every other day for 3 weeks, then  $\frac{1}{2}$  spider for one week and finally  $\frac{1}{3}$  spider for one week, at the same intervals.

These rats were next tested for resistance by being given first, tentatively, one spider each, which they accepted without any symptoms, 3 days later 2 spiders each were given, again without effect, and finally 3 days later 4 spiders each. No symptoms whatever occurred and we concluded that either tolerance or immunity had been achieved.

*In Vitro Neutralization.* The resistance indicated in the preceding paragraph might be interpreted either as tolerance

blood was permitted to clot and the serum decanted. Various mixtures of serum and venom were prepared, as summarized below, and permitted to stand in the cold over night and then injected intraperitoneally into young rats (50 to 60 grams).

Preparation I. The venom from 10 spiders in 1 cc. saline plus 1 cc. immune serum.

Preparation II. The venom from 10 spiders in 1.5 cc. saline plus  $\frac{1}{2}$  cc. immune serum.

TABLE 20

MATERIAL INJECTED	NO. OF RATS	AMOUNT OF VENOM	RESULTS
Prep. I	3	Equiv. of 2 spiders (8 A.L.D.)	No symptoms
Prep. II	4	" " 2 "	" "
Prep. III	2	" " 2 "	All died
Prep. III	2	" " 1 "	" "
Prep. III	2	" " $\frac{1}{2}$ "	1 died; 1 recovered

TABLE 21

MATERIAL INJECTED PER RAT		INTERVAL BETWEEN VENOM AND SERUM INJECTIONS	NO. OF RATS	RESULTS
Venom	Serum			
Equiv. of 1 spiders (8 A.L.D.)	1 cc.	10 minutes	4	No symptoms
" " 2 "	$\frac{1}{2}$ cc.	10 "	4	" "
" " 2 "	1 cc.	1 hour	4	Recov'd. promptly
" " 1 "	1 cc. normal serum	10 minutes	4	All died

or as true immunity due to anti-body formation. To test which of these conditions obtained, 5 rats of each group were bled to death and the sera pooled. In other experiments we have found that the most satisfactory way to obtain the largest possible amount of blood was to cannulate the carotid, the cannula being attached to a large syringe. Gentle suction exerted by the plunger fills the syringe rapidly and clotted needles are avoided. From 8 to 10 cc. of blood is easily obtained from adult rats. This procedure was therefore employed. The

Preparation III. The venom from 10 spiders in 1 cc. saline plus 1 cc. serum from normal (non-immunized) rats.

Results of the injection are shown in Table 20.

The above results agree with the work of Troise, indicating that direct neutralization of the venom takes place.

*Direct Injection.* The remainder of the serum obtained as described above was tested by direct injection into animals injected with venom. The results are given in Table 21.

In the third group symptoms were well

advanced by the time the serum was given. In large doses (1-2 spiders) symptoms start promptly and death may occur within 2 hours. Relief seemed to be very prompt, the animals appearing normal, except for slight residual paralysis of the limbs, within 2 hours after introduction of the serum.

The above experiment was repeated, using 8 of the remaining rats. During the two weeks interval these had been given  $\frac{1}{2}$  spider each every other day. The results are given in Table 22.

Attention is directed to the last group as simulating more exactly the condition encountered in the human case of arach-

The results of these experiments may be summarized as follows:  $\frac{1}{10}$  cc. of serum given immediately (less than 10 minutes) protects rats against the venom of 2 spider equivalents (8 A.L.D.), both being given intra-peritoneally. 1 cc. of serum will protect rats against 2 spiders if given one hour later.  $\frac{1}{2}$  cc. given one hour later will not protect in all cases, both being given intra-peritoneally. If the venom be given sub-cutaneously, 1 cc. of serum (given intra-peritoneally) will protect against 2 spiders even though administration be delayed for three and one-half hours. It should also be pointed out that the upper limits both for direct

TABLE 22

MATERIAL INJECTED		INTERVAL BETWEEN VENOM AND SERUM INJECTION	NO. OF RATS	RESULTS
Venom (Spider Equiv.)	Serum			
2 (8 A.L.D.)	$\frac{1}{2}$ cc.	10 minutes	4	No symptoms
2     "	$\frac{1}{10}$ cc.	10     "	4	Slight paralysis, not really sick, prompt recovery
2     "	$\frac{1}{2}$ cc.	1 hour	4	3 recovered; 1 died
2 Inj'd. Sub-cut.	No serum		4	All died
2 Inj'd. Sub-cut.	1 cc. Intraperitoneally	3 $\frac{1}{2}$ hours	4	All recovered

nidism. When the venom is given sub-cutaneously, the symptoms are slower in making their appearance, the length of life following lethal doses is increased and the absolute lethal dose somewhat greater. At the end of three and one-half hours symptoms are, however, well advanced. The rats are comatose, bloody serum covers the nose, respiration is slow and paralysis is present. The injection of serum intra-peritoneally gives prompt relief, within 3 to 4 hours the rats are again normal. It is probable that intravenous injection of serum would give even better results, but this is difficult to perform in small rats without risking the danger either of heart puncture or anesthesia.

protection and for protection against sub-cutaneous injection of venom have not been reached, the figures given merely represent the lowest dosages of serum used. It is very probable that the serum is even more active than these figures indicate.

*Placental Transmission of Anti-bodies.* Two rats of the immunization series became pregnant and had their litters about the time that the last group was sacrificed (about 12 weeks immunization). The litters were saved until they reached a weight of 50-60 grams and were then injected, along with controls, as indicated in Table 23.

This would apparently indicate some degree of transmission of antibodies, either through the placenta or in the

milk, although the immunity is not of very high grade.

*Immunization with Eggs and Cross-immunization.* Parallel with the venom-immunized rats, another group was injected with sub-lethal amounts of eggs. Injections were commenced with  $\frac{1}{2}$  egg each week for five weeks. Immunization appeared rather more promptly than in the venom-immunized group; tests with lethal doses at the end of five weeks caused slight symptoms only. Injection of two eggs per dose was given twice

saline mixed with 5 cc. serum from venom-immunized rats.

Prep. III: 50 eggs macerated in 5 cc. saline mixed with 5 cc. normal serum.

Prep. IV: Glands from 10 spiders macerated in 1 cc. saline plus 4 cc. serum from egg-immunized rats.

Results of the assay are given in Table 24.

The results show a neutralizing action of homologous serum upon the egg poison, and also that the two poisons are distinct; neutralization of egg poison by

TABLE 23

RATS USED	NO. OF RATS	AMOUNT OF VENOM	RESULTS
From Immunized Mothers	3	1 spider	2 died; 1 sick but recovered
" " "	3	$\frac{1}{2}$ "	Sick but recovered
Controls	3	1 "	All died
"	3	$\frac{1}{2}$ "	" "

TABLE 24

MATERIAL INJECTED	AMOUNT OF POISON	NO. OF RATS	RESULTS
Prep. I	Equiv. of 5 eggs	4	No symptoms
Prep. II	" " 5 "	4	All died
Prep. III	" " 5 "	3	" "
Prep. III	" " $2\frac{1}{2}$ "	3	" "
Prep. IV	" " 2 spiders	2	" "
Prep. IV	" " 1 "	2	" "

weekly for an additional five weeks, when the animals were tested for immunity. A maximum of 16 eggs per rat gave slight symptoms only with prompt recovery. Control rats of the same weight were killed by 8 eggs.

The serum from sacrificed rats was next tested for its neutralizing power in vitro. The following mixtures were prepared and permitted to stand over night.

Prep. I: 50 eggs macerated in 5 cc. saline, mixed with 5 cc. serum from egg-immunized rats.

Prep. II: 50 eggs macerated in 5 cc.

venom-immunized serum does not occur, nor does the reverse.

Direct injection of egg-immunized serum is also protective, as is shown in Table 25; the limit of protection was not tested for.

*Commercial Anti-serum.* From the results described in the previous section, the commercial preparation of an anti-serum against the venom of the black widow appeared to be feasible. Even though the fatality rate in arachnidism of this type is low, the fact remains that it is occasionally fatal. Our work indicates

that a bite would be more likely to be fatal in children and young children are particularly likely to be bitten, being ignorant of the danger and curious as to the spider. Aside from the prevention of a fatal outcome, the promptness with which symptoms disappear in the rat following the administration of serum

assay, made after about ten weeks injection, are given in Table 25a.

These results indicate that already a serum of considerable potency has been produced, although, of course, its efficacy in the human remains to be demonstrated by clinical trial. This work is being continued.

TABLE 25

MATERIAL INJECTED		NO. OF RATS	RESULTS
Eggs	Serum		
2	None	4	All killed
5	1 cc. within 10 minutes	3	No symptoms
10	1 " " 10 "	3	No "

TABLE 25a

NO. OF RATS	VENOM		SERUM		RESULTS
	Amount	Mode of Injection	Amount	Mode of Injection	
4	$\frac{1}{2}$ spider	Intra-per.	None		3 killed
4	$\frac{1}{2}$ "	"	"		All "
2	2 "	"	$\frac{1}{2}$ cc. #2	Intra-per. in 5 min.	Recovered
2	2 "	"	$\frac{1}{2}$ cc. #3	" " " "	"
4	2 "	"	$\frac{1}{2}$ cc. #2	" " " "	"
4	2 "	"	$\frac{1}{2}$ cc. #3	" " " "	"
4	2 "	"	$\frac{1}{10}$ cc. #2	" " " "	All died
4	2 "	"	$\frac{1}{10}$ cc. #3	" " " "	Recovered
2	2 "	Sub-cut.	None		Died
2	2 "	"	$\frac{1}{2}$ cc. #2	" " " "	"
2	2 "	"	$\frac{1}{2}$ cc. #3	" " " "	1 died
2	2 "	"	1 cc. #2	" 3 $\frac{1}{2}$ hours	Recovered
2	2 "	"	1 cc. #3	" " "	"

would further recommend it as a therapeutic agent.

We were fortunate in interesting the E. R. Squibb and Sons Company in the problem and a cooperative project was undertaken, in which we collected the spiders and sent them the dried venom glands. They began the injection of two sheep in the late summer, starting with small doses of venom and gradually increasing the dose. The results of the first

### Toxicology

*Symptomatology.* The effect of the black widow spider venom upon the organism has been variously described by different investigators. In the human Bogen (2) has studied a considerable series of cases and finds that the chain of symptoms is a remarkably constant one. The outstanding features in the sequence of events are as follows: The bite itself is not painful,

being comparable to a sharp pin prick; a dull numbing pain ascends the extremity bitten, and then localizes itself in the muscles of the chest, back and abdomen. This pain is excruciating in character. The abdominal wall is board-like in its rigidity; except for the absence of local tenderness and the involvement of other muscle groups the pain resembles that experienced in the case of a ruptured appendix or perforated peptic ulcer. Due to the spasm of the thoracic muscles respiration is difficult. A rise in blood pressure occurs, there is frequently nausea and vomiting, a slight fever and leucocytosis. The general symptoms make their appearance within four hours and may last for two to three days. In fatal cases death occurs in from 18 to 36 hours. The observations are in general agreement with those of Baerg (7) and of Blair (1) who permitted spiders to bite them under controlled conditions. Relief from pain seems to be difficult to obtain, relatively large doses of morphine are without much effect; hot baths are very helpful.

In the rat, administration of the venom is followed by paralytic symptoms which are first evidenced by a peculiar stiffness of gait and awkwardness in movement. The hind legs are first affected and the animal walks with the rear elevated. One or both forelegs are next affected and the animal sits in a hunched up position with the forelegs bent and held close to the body. At this time the animal refuses to move unless violently stimulated but can withdraw the foot if the toes be pinched. As regards respiration, we noted a difference in behavior usually depending upon the size of the animal. In immature rats the respiration becomes progressively more and more shallow, the animal lies in a state of coma; as death approaches, the breathing becomes almost imperceptible. In older rats respiration

becomes extremely labored. The animal gasps violently for air but is apparently unable to fill the lungs. This labored respiration continues until death occurs. Many rats were autopsied immediately after death. In all cases the lungs collapsed when the thorax was opened, indicating no constriction of the bronchioles, although, as will be noted later, ephedrine appeared to give considerable relief. The auricles were usually beating. There were no gross signs of pathologic changes.

One effect which was invariably produced was an irritation of the lachrymal glands. The eyes watered profusely; they were usually closed or nearly so. There was always an accumulation of bloody serum around the nostrils, frequently in considerable amounts. This happened even when there was no labored respiration. The animals suffered from thirst and in the earlier stages made efforts to drink but were apparently unable to swallow.

*Antidotes.* No extensive study of antidotes was possible in the time available; however, a few drugs which for one reason or another suggested themselves, were tested. So far as we are aware no specific antidote is known. Mature rats (200-250 grams) were used in the following experiments. Table 26 summarizes the results.

Sodium amytal and scopolamine were used because of their depressant action upon the central nervous system. Dinitrophenol was tried in the hope that the high basal metabolism which it induces might lead to a more rapid destruction of the venom. Methylene blue was tried because one experiment in which the venom was hydrolyzed and tested with Fehling's solution gave a positive test. (This result could not be confirmed later, but at the time suggested the possibility that a

glucoside bearing a cyanide group might be responsible.) Congo Red was employed because of its known action of absorbing bacterial toxins. Curare, because it seemed possible that its paralytic effect on skeletal motor plates might be antagonistic to the possible irritating effect of the toxin.

The only agent which seemed to be of value was ephedrine; however, only three animals were used and it was unfortunately too late to conduct an extensive experiment. Its action was apparently to

eggs, they refused to drink the water solution, but ate the food containing eggs in amounts up to 20 eggs each, also without effect. In view of the results reported under chemistry, the destruction of the venom probably takes place in the stomach, being effected by the acid present. The egg globulin is presumably destroyed in digestion.

*Effects upon Blood.* Red and white counts and coagulation time determinations (capillary) were made every other day for one week on four rats. Two were

TABLE 26

NO. OF RATS	ANTIDOTE TESTED	AMT. VENOM	RESULTS
12	No Antidote (Controls)	Equiv. of 2 spiders	All died
5	Sodium Amytal 12.5 mg.	" " 2 "	4 died, 1 recovered
4	" " 6 mg.	" " 2 "	All died
3	Scopolamine hydrobromide 1/50 grain	" " 2 "	All died, the treated animals lived 2 days longer
2	Dinitro phenol 4 mg.	" " 2 "	Died sooner than the controls
3	Methylene blue 2-4 cc. 1% solution	" " 2 "	All died
2	Congo Red 2-4 cc. 1% solution	" " 2 "	" "
3	Curare 2 mg.	" " 2 "	" "
1	Ephedrine sulfate 6 mg. in 2 doses ½ hour apart	" " 2 "	Recovered
2	Ephedrine sulfate 3 mg. (1 dose)	" " 2 "	1 died; 1 recovered
2	Calcium gluconate 20 mg. immediately plus 20 mg. ½ hour after venom injection	½ spider each	Both died
(wt. 50 grams)			

give relief from the extreme dyspnea. This experiment should be repeated and extended.

*Oral Administration without Effect.* Food and water was withheld from 8 rats, the former for 48 and the latter for 24 hours. Four rats were then given small amounts of water containing venom and corn meal moistened with a venom solution, which they consumed readily. The total amount consumed within thirty minutes was the equivalent of 8 spiders each. No effects whatever were observed. The other four rats were given macerated

then injected daily for four days with sub-lethal doses of venom and the other two with sub-lethal amounts of eggs. The amount given varied with the condition of the animals, but was sufficient to keep them in an almost moribund condition. Red and white counts and coagulation time determinations were made in duplicate daily during the injection period. The results are shown in Table 27.

The red count was not affected. The white count, as might be expected, fluctuated widely; generally speaking, however, there was a slight leucocytosis during



the first day or two of the injection period, which later subsided. The coagulation time was increased somewhat, probably not significantly.

*Body Temperature.* The rectal temperatures of 2 rats were taken at 15 to 30 minute intervals following the injection of lethal doses of venom. A progressive fall of about one-half degree per hour

a venom solution (in saline) neither increased nor decreased its irritability. 3. An entire muscle-nerve preparation soaked for 30 minutes in a saline solution of venom behaved the same as a control preparation kept for an equal length of time in saline. These findings, which are by no means conclusive, support the view that the action of the venom upon

TABLE 27

POISON INJECTED	RED COUNT IN MILLIONS				WHITE COUNT IN THOUSANDS				COAGULATION TIME (MIN.)			
	Control Period		Injection Period		Control Period		Injection Period		Control Period		Injection Period	
	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High
Rat #16 Eggs	9.6	11.3	9.2	9.4	8.1	8.7	6.6	10.6	1.40	1.50	1.45	2.45
Rat #6 Eggs	8.4	10.0	8.9	9.3	6.0	12.0	7.5	13.0	1.50	2.00	1.50	2.5
Rat #76 Venom	7.4	10.0	8.3	9.6	8.1	10.6	8.0	13.7	1.40	1.50	2.05	2.5
Rat #11 Venom	8.6	9.6	8.5	9.0	6.0	8.7	9.0	15.0	1.35	1.50	2.00	3.20

TABLE 28

FRESH EGGS		DRIED PRECIPITATE	
Concentration	Time	Concentration	Time
1:100	20 seconds	1:2000	1 minute, 10 seconds
1:100	20 "	1:4000	2 " 15 "
1:500	35 "	1:6000	5 " 30 "
1:1000	55 "	1:8000	8 " 40 "
1:1000	1 minute, 55 "		
1:4000	5 "		
1:10000	25 "		

resulted, reaching just before death a level of 94.6 in one and 93.6 in the other rat.

*Muscle Nerve Preparation.* Several experiments were performed in which the effect of venom upon muscle-nerve preparations of the frog was studied. The results were negative and may be briefly summarized. 1. Injection of venom directly into the muscle caused no contraction. 2. After testing for the minimum effective electrical stimulus, soaking the nerve in

the musculature is by way of the central nervous system rather than peripherally.

*Hemolytic Action of Egg Poison.* Studies of the rate of hemolysis of the protein from fresh eggs, and of the dried, precipitated protein were made, also of the anti-hemolytic action of the serum from egg-immunized rats. A suspension of rat red cells was used in these experiments. The results are given in Table 28.

The 1:6000 concentration of dried egg precipitate was used as the test solution

for the study of the anti-hemolytic action of egg-immunized serum. The results are given in Table 29.

Since at this dilution the hemolysin is effective within 5 minutes and 30 seconds, it can be stated that the anti-hemolysin is capable of neutralizing it at a concentration of 1:10,000.

TABLE 29

CONCENTRATION OF SERUM	TIME
1:20	Had not occurred at end of 2 hours
1:100	" " " " " 2 "
1:500	" " " " " 2 "
1:1000	40 minutes
1:5000	30 "
1:10000	8 "

### Pathology

Several rats were kept chronically intoxicated with venom for four days. They were then killed by administration of a lethal dose, the following structures removed and sectioned: heart, lungs, liver, spleen, stomach, small and large intestines, kidneys, adrenals, gonads, brain, and spinal cord. Histological study of these sections revealed very little; small areas of necrosis in the liver and a few swollen and hyper-chromatic cells in the motor region of the brain and anterior horns of the chord being the only pathologic findings. A rat was then kept intoxicated for two weeks, being given approximately 8 spiders during this period. The original weight was 188 grams, the final weight 121 grams. Autopsy revealed no gross pathologic lesions. The same structures as listed above (ovary and uterus) were removed and sectioned. Again very small necrotic areas in the liver were found. Special staining methods were employed for the central nervous system, but no pathologic abnormalities

could be discovered. No significance is attached to the liver injuries as they were slight and might have been due to other causes.

These studies were carried out at the University of Colorado School of Medicine, under the direction of Doctor James J. Waring, to whom our great appreciation is herewith expressed.

### DISCUSSION

The questions we have been asked most frequently as the fact of our investigation of the spider became known were these: 1. Are the spiders increasing greatly in numbers? 2. Is the spider changing its habits, that is, is it leaving its rural haunts and invading settled communities to a greater degree than before? 3. What methods of eradication are feasible? 4. Does the spider represent a real menace? 5. Is there any effective antidote? 6. What are the possibilities of anti-venin? To the first question the authors do not hesitate to give an affirmative answer. This may appear unjustified since this is admittedly the first year in which we have collected the spider. If the black widow were smaller, if its appearance were not so striking, if it were easily confused with some other form, or if it had previously been fairly common, one might hesitate to commit himself. However, as an example, we have a cold box set just outside the laboratory, on the ground level, and opening into the room by means of a window. So far, we have on two different occasions found three spiders at one time and another time two spiders, in webs close to the window. They are visible all the way across the room. When opening the window, one must be blind not to see them. This box has been there for years. We feel morally certain that had spiders ever been in the

same location before we would have noticed them.

It is of course true that one sees what one looks for, and the newspaper publicity which these spiders have received has caused many more of them to be noticed and reported than would otherwise have been the case. On the other hand, farmers and fruit growers are usually quite observant as to the kind of insects found on their crops and when this year, for the first time, reports are received that tomato growers find the spiders so bad that protective clothing must be worn, when grape growers report that in some places the spiders are so numerous that the pickers refuse to work, and the grapes are rotting upon the vines, and peach growers notice many of them in their orchards, the conclusion seems inescapable that they are more numerous this year than ever before.

The second question, relating to an apparent change in the habits of the spider, in that it seems to be invading settled communities to a greater degree, is to some extent dependent upon the first. If the spiders in a given region increase greatly in numbers, their manner of dispersal by wind and their utilization of such means of transportation as box cars would make it inevitable that some would find themselves within towns and cities. Once having become established, their chances for survival and increase are favored. Many of them have been found in basements, garages and similar places where they are protected against the cold to a much greater degree than would be the case out in the open. We believe that the increase in numbers noted during the past summer is due to the mild winter which preceded it; however, cold will not operate as a check upon those which have established themselves in the garages and basements of heated buildings. The conclusion appears inescapable that, unless

drastic methods of eradication are employed, we will have a considerable, and probably an increasing number of these unwelcome guests.

This leads to the problem of eradication. We have tested, under laboratory conditions, several of the more common insecticides. The general conclusion was that such insecticides as Flit and Black Flag, in concentrations sufficient to kill promptly all flies within the room, is without effect upon spiders, as would be expected from the difference in the anatomy of the respiratory organs. Sulfur dioxide, in high concentration, will kill them in time, as will carbon disulfide, though relatively high concentrations and long exposures are necessary. Often the spider appears to be dead and remains so for hours but eventually recovers. Hydrogen cyanide, in the form of cyanogas, is effective, but too dangerous to recommend for general use. The California State Department of Health recommends the use of creosote and crude oil sprays, which would no doubt be effective in certain locations, but are obviously unavailable in vineyards or tomato beds. The spider is far from gregarious in its habits and consequently a given basement or garage will not harbor more than perhaps a half dozen. Our suggestion, when called upon for advice, has been to locate the individual spider, easiest done at night, and destroy it, rather than resort to general fumigation. This advice is valueless for the aforementioned farmer or fruit grower; protective clothing during the picking season and burning of debris afterward is about all that can be suggested.

Does the spider represent a real menace? We have emphasized throughout, in our dealings with the press and public, the fact that the spider is above all extremely timid. We have rarely seen a spider,

disturbed in her web, who made any pretense of defense, to say nothing of attacking. They will almost invariably run and hide and remain out of sight in a crevice or hole for hours afterward. The danger lies in accidentally squeezing one when picking up some object to which the spider is clinging, when putting on old clothing left hanging in a shed, or in some similar way. Some children enjoy catching and playing with crawling things, which cannot be done with impunity with the black widow. As to the bite itself, there can be no question of its frequently serious, sometimes fatal, effects. The statement sometimes heard, even from zoologists who should know better, that the bite of a black widow is no more dangerous than that of a mosquito, must, in view of extensive clinical experience, be branded as false and dangerous.

There is, at present, no effective antidote. First aid treatment might well comprise the application of a tourniquet, free incision and the sucking out of the venom either by means of the mouth or some mechanical device. However, as Bogen has emphasized, the spider usually lives in filthy surroundings and the danger of infection is consequently great. Thorough sterilization of the site of the wound should therefore precede incision. Further treatment is best carried out in a hospital; it consists mainly of measures taken to alleviate pain, the free use of morphine, hot baths, etc.

*The possibilities of anti-venin.* Bogen gives data on the use of convalescent serum in a series of cases in California, from which he concludes that its use has to some extent aided the patient; however, it is doubtful whether the number of cases is adequate to prove the point statistically. At least as far as the rat is concerned immunity develops very slowly; it will be recalled that five weeks

injection of sub-lethal doses granted little, if any, protection and that it was necessary to continue the injections for nearly three months before a really high grade immunity was developed. It is, of course, quite possible that immunity develops more rapidly in the human, but it seems doubtful that convalescent serum would ever contain as high a concentration of anti-bodies as could be produced artificially. The question of ready availability of convalescent serum must also be considered. In California, with its relatively high incidence of arachnidism, this might not present a problem, but in other regions the situation would be more difficult.

In this connection, a letter received from the mother of a spider victim is of interest. She states that her son was bitten upon the leg two summers ago. He became seriously ill, showing the typical symptoms, but recovered. Last summer he was again bitten, this time on the hand, he again was very ill but recovered. The interesting point is that the site of the first bite became badly swollen and painful at the time of the second bite, apparently indicating a local sensitization to the venom.

The serum at present being developed by the E. R. Squibb and Sons Company must await clinical use before its efficacy in the treatment of arachnidism will be known. The potency already obtained compares well, on the basis of lethal doses neutralized, with certain commercial snake antivenins. It appears likely that the principles involved in the use of snake antivenin, particularly the time factor, will apply to spider antivenin. If, as Blair believes, the absorption of the venom is by way of the lymphatics, it seems probable that superficial injection of the antiserum immediately, in the immediate vicinity of the bite, offers the best hope of success.

## SUMMARY

An investigation of the natural history of the black widow spider and certain properties of its venom are described. The salient points resulting from this study are:

1. The appearance of the spider is illustrated by plates and certain of its breeding, nesting, and distribution habits described.
2. The toxicity of the venom was accurately determined.

3. Chemical studies indicate the toxic principle to be a protein, probably an albumen.

4. Various antidotes were tested, the tests resulting negatively.

5. The preparation of a potent anti-venin from the rat is described and a preliminary report covering similar results in the sheep is presented.

6. The venom is shown to be chemically and serologically distinct from the poisonous principle of the eggs.

## BIBLIOGRAPHY

1. BLAIR, ALAN; 1934. Spider poisoning. *Archives of Internal Medicine*, vol. 54, p. 831.
2. BOGEN, EMIL; 1932. Poisonous spider bites. *Annals of Internal Medicine*, vol. 6, p. 375.
3. BURT, CHAS. E.; 1935. A review of the biology and distribution of the hourglass spider. *Journal Kansas Entomological Society*, vol. 8, no. 4, p. 117.
4. PHILLIP, CORNELIUS B.; 1935. Arachnidism, black widow spider poisoning. *Northwest Medicine*, vol. 34, p. 52.
5. LAWSON, P. B.; 1933. Notes on the life history of the hourglass spider. *Annals of the Entomological Society of America*, vol. 26, no. 4, p. 568.
6. IRVING, WILLIAM G., AND HINMAN, E. HAROLD; 1935. *Science*, vol. 82, no. 2130, p. 395.
7. BARRG, W. J.; 1922. The effects of the bite of *Latrodectus mactans*. *Journal of Parasitology*, vol. 9, p. 161.
8. TREVAN, J. W.; 1927. Error of determination of toxicity. *Proceedings of the Royal Society, Series B*, vol. 101, p. 483.
9. COWARD, K. H., AND BURN, J. H.; 1927. Errors in biologic assays. *Journal of Physiology*, vol. 63, p. 270.
10. D'AMOUR, F. E., AND GUSTAVSON, R. G.; 1930. A critical study of the assay of female sex hormone preparations. *Journal of Pharmacology and Experimental Therapeutics*, vol. 40, no. 4, p. 473.
11. LEVY, R.; 1916. Contribution à l'étude des toxines chez les araignées. *Paris Annales des Sciences naturelles Zoologiques*, Series 10, p. 161.
12. SZU, C., AND WU, H.; 1934. Fractional precipitation of serum protein with methyl alcohol. *Chinese Journal of Physiology*, vol. 8, p. 97.
13. TROIER, E.; 1928. Sérum actif contre le venin de l'araignée *Latrodectus mactans*. *Comptes Rendus, Société de Biologie*, vol. 99, p. 1434.





# THE PROBLEM OF CYCLOPIA

## PART I

By HOWARD B. ADELMANN

*Department of Histology and Embryology, Cornell University, Ithaca, N.Y., and Department of Ophthalmology, Columbia University, New York City*

### I. INTRODUCTION

THE history of teratology, which is concerned primarily with the study of abnormal or monstrous forms of development, parallels in a general way the history of embryology itself, since it is essentially but a subdivision of the latter. It, too, was blighted by the doctrine of preformation, but it suffered, in addition, a series of handicaps from which it has only recently been freed. In spite of the fact that Aristotle, with characteristic acumen, had insisted that 'monstrous' forms must arise in conformity with natural laws manifested in an unusual way, the notion tenaciously persisted that developmental abnormalities were the result, if not of supernatural, at least of phenomena which were not to be accounted for by the operation of the ordinary and accepted 'laws' of development.

The subject was in a truly chaotic state in the early part of the nineteenth century when, through the studies of Etienne and Isidore Geoffroy St. Hilaire (1826, 1832-37), some order was brought into the confusion which existed as to the interpretation of anomalous development. They first made clear that abnormalities may be classified into fairly well-defined types. While there is no sharply defined delimitation of types each exhibits a rather uniform plan of organization. They also showed (1826, 1832-37) that the course of development might be experi-

mentally modified with the resultant production of abnormal forms similar to those spontaneously occurring and hitherto sometimes ascribed to an abnormal preformation of the germ.

Some years later this achievement was followed by an equally great one of a countryman of theirs, Dareste, who in a truly remarkable work published in 1877, described the successful experimental production of monsters on a large scale, but more important than this, pointed out clearly the logical approach to their study.

The anomaly and the monstrosity appear at certain epochs of development as a result of a modification in the evolution of an isolated organ or of a more or less considerable number of organs. They are the result of a change in the direction of the force which determines the successive appearance and the coordination of different parts of the embryo. The teratogenesis, or in other words, the embryogenesis of anomalous beings, must then consist, like that of normal beings, of direct study of the successive changes which development determines in the organism.

Time has only served to emphasize the essential soundness of Dareste's position.

Much of the indifference with which the modern embryologist tends to regard the study of abnormal development is due to the fact that in the past premature efforts have been made to ascertain a specific 'cause' for an anomaly, disregarding the fact that an anomaly usually represents a response of the developing organism to unusual or abnormal conditions, and that a variety of environmental factors by evok-

ing a relatively slight deviation from the normal in relatively early stages of development, may entail a series of increasingly serious developmental aberrations in later stages due to the suppression of, or interference with, normal developmental interactions and correlations, some of which have recently been so beautifully demonstrated by experimental workers in embryology. When the conditions under which specific anomalies are produced have been determined, the developmental aberrations described when they first appear, and their influences upon the later progress of developmental correlation and integration ascertained in the light of what is known to occur during normal development, progress has at least been made in their elucidation. The determination of a 'first' or 'primary cause' may well await a more complete knowledge.

While progress in the study of anomalous development must, for the most part, follow after advances in the knowledge of normal development, the operation of the factors influencing normal development may often be made more vivid by a demonstration of the consequences of their abnormal manifestations. In illustration one might cite the work of Holtfreter ('33d) who has demonstrated by the study of amphibian exogastrulae the profound effect of the roof of the archenteron upon the differentiation of the neural plate, a fact which had been previously made clear by Spemann's ('24, '31) researches, but which is now made possibly more convincing. Holtfreter's ('33c) work now makes possible a great advance in the interpretation of certain forms of anomalies the genesis of which has hitherto not been clearly understood.

Another equally interesting illustration is afforded by Cyclopia, an anomaly which for a long time has engaged the attention

of embryologists, and to an analysis of which the present review will be devoted.

### *The Morphology of Cyclopia*

Cyclopia is an anomaly, the salient characteristic of which is the presence of a single median eye situated in the middle of the face in the position normally occupied by the nose. It is to be distinguished from *monophthalmia asymmetrica* characterized by the presence of a single, laterally placed eye, its counterpart having failed to develop.



FIG. 1. CYCLOPEAN WOMAN FROM REISCH'S *MARGARITA PHILOSOPHICA*, BASEL, 1508

Cyclopia has, doubtless, occurred among all the vertebrates, including man, since first they were evolved, and the deep impression it made upon the minds of the ancients is attested by the fact that the term itself is derived from Homer's mythical race of one-eyed giants, the Cyclops, who, we are probably safe in assuming, have some basis in fact. Hesiod, too, mentions the Cyclops, as does Pliny, and since then literature is rich in allusions to that picturesque, though imaginary race.

Aristotle, strangely enough, does not describe cyclopia but descriptions of cyclopean monsters are not uncommon in the writings of the natural philosophers of the sixteenth and seventeenth centuries. They are, however, typically inaccurate

and often fanciful. For example, in the figure of a cyclopean woman, published by Gregor Reisch in his *MARGARITA PHILOSOPHICA* in 1508, (fig. 1), the eye is placed *above* the nose, a condition never actually realized as will be pointed out later. The figure further passes the bounds of credence in that the cyclops is represented as a mature woman, while the figures grouped about her bear further witness to the gullibility characteristic of writers of the period. Another, more nearly accurate figure with respect to the



FIG. 2. THREE VIEWS OF A CYCLOPEAN INFANT FIGURED BY LICETUS IN HIS *DE MONSTRORUM CAUSSIS*, ETC., 1634

In contrast to Reisch (fig. 1) the nose is correctly placed above the incompletely cyclopean eye. A fanciful feature is the depiction of two eyes on the dorsal side of the head, as shown in the view on the left.

relation of nose and eye, taken from the second edition of Licetus' (1577-1657) *DE MONSTRORUM CAUSSIS* (1634), is reproduced in figure 2. The description of two eyes in the dorsal side of the head of this specimen is doubtless based on a misconception.

Relatively few descriptions of cyclopia were published during the eighteenth century (Ballantyne, '04). They are, for the most part, contained in rare publications, not represented even in fairly large collections and, therefore, rather inaccessible. Judging from references in

Meckel (1826) and Huscke (1832), however, many of the eighteenth century publications present rather complete and creditable anatomical descriptions of the anomaly. A voluminous literature has, however, appeared since the beginning of the nineteenth century. No attempt will be made to exhaustively review it since it consists in large part of purely gross anatomical descriptions of the anomaly in various animals, accompanied by oftentimes unsound speculation as to its causes. Due to the interest the subject has aroused we are now provided with fairly adequate descriptions of the anomaly in almost every vertebrate class (reptiles excepted?), references to which are to be found in the works of Ballantyne ('04), Schwalbe ('13), Seefelder ('27), and Wright and Wagner ('34). A survey of the literature reveals the important fact that just as in all vertebrates a fundamentally similar plan of organization exists, so too, cyclopia exhibits an essentially similar pattern or, in other words, a characteristic deviation from the normal pattern, in all vertebrates (figs. 3 to 5, 12c). In this lies the peculiar importance of the anomaly from an analytical viewpoint. It permits, too, a generalized description which in its essential features holds true for all forms.

In so called *cyclopia perfecta* the eye is perfectly single in all its parts (Ballantyne, '04, p. 395), possessing a single cornea, pupil and lens, and revealing in other respects also no evidence of doubling (figs. 3, 4, 8, 10). The single median eye, however, is but one component of a complex of abnormalities affecting the entire prechordal region of the head (Cotronei, '22, b; Adelmann, '34), all of which must be considered for an adequate conception of the nature of the anomaly. The external nose is often lacking, or when present is situated *above* the eye. (Allan's ('48) case is probably no exception). The



nasal chamber, too, is single, often failing to communicate with the pharynx. The brain exhibits such constant and typical malformations that Schwalbe and Josephy ('13) regard them as constituting the most characteristic feature of the anomaly. The forebrain, in perfect cyclopia, is never divided into hemispheres but consists of a simple sac enclosing an undivided ventricle, the diencephalon also being markedly abnormal in form to varying degrees. The midbrain, however, may approximate the normal. The more caudal subdivisions of the central nervous

physis is present in cyclopia perfecta. It is usually absent (Phisalix, '89) and where its presence is reported the eye shows some evidence of doubling. The epiphysis may be present or absent.

The optic nerve is variable in behavior, being sometimes present as a single strand, or often entirely absent. In younger stages the eye is often attached to the brain by the tapetum (pigment layer of the retina) with no indication of the presence of an optic stalk (Speimann, '04; Stockard, '09b; Fischel, '11, *et al.*).



FIG. 3. CYCLOPEAN RAY, MEASURING 20 CM. TO THE BASE OF THE CAUDAL FIN, DESCRIBED BY PAOLUCCI, '74

FIG. 4. CYCLOPEAN DUCK FROM BLUMENBACH'S COLLECTION, ILLUSTRATED BY HUSCHKE, 1832.

The protuberance above the eye is the nose.

FIG. 5. CYCLOPEAN HUMAN FETUS WITH WELL-FORMED JAWS AND MAXILLARY REGION (VROLIK, '49)

There was but a single optic nerve.

system, disregarding certain deviations in the pattern of the tracts, are rarely affected, except in cases where the embryo as a whole exhibits evidences of severer and more or less generalized abnormalities (Stockard, '10a). Stockard ('09b), however, believes that in *Fundulus* cyclopia may be accompanied by a perfectly normal forebrain. If this is so the fishes constitute an exception to a rule which seems to hold invariably in other forms, and even for some fishes according to Gemmill ('06) and Werber ('16b).

It is still doubtful whether the hypo-

The olfactory nerve, or rhinencephalon, also may be present as a single rudimentary tract or entirely absent.

The third to the twelfth cranial nerves are usually present. The third and fourth are occasionally absent (Chidester, '14) and when present sometimes anastomose medially (Phisalix, '89, Mall, '17), a condition possibly correlated with fusion of the eye muscles. The latter are apparently variable in development, an interesting feature being the tendency of those innervated by the oculomotor nerves to fuse (Wilder, '08; Mall, '17).

It is perhaps unnecessary to remark that the skeletal elements of the head are also abnormal, but since these abnormalities are, in all likelihood, secondary to antecedent malformation of the eye, olfactory organ and brain, they need not be dwelt upon. Detailed accounts will be found in Schwalbe ('13), Ballantyne ('04), and Wright and Wagner ('34).

The marked tendency for cyclopia to be accompanied by malformations of the mouth, lower jaws and, in severer forms, of the maxillary region in the condition commonly known as otocephaly (fig. 6) is,

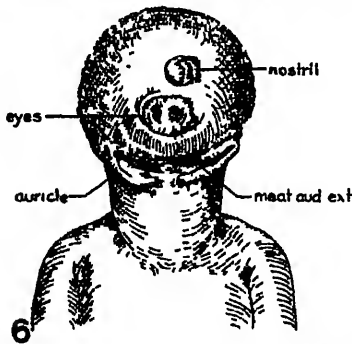


FIG. 6. OTOCEPHALIC HUMAN FETUS (STREETER, '12)

In addition to a high degree of synophthalmia there is a complete arrest in the development of the greater part of the mandibular arch, with the result that the auricles maintain their original embryonic position.

as will subsequently be pointed out, probably a feature of fundamental significance. The abnormalities of the mouth and lower jaws of Stockard's ('09b) cyclopean *Fundulus* embryos are evident in figure 8. Otocephaly, as defined by Josephy ('13) is a condition characterized by the rudimentary development or complete lack of the lower jaw. The mouth is consequently often imperfectly developed and the ears show a tendency to approximate or fuse. While otocephaly need not necessarily accompany cyclopia, the coincidence is so marked that it is difficult to escape the suspicion that the two

anomalies are closely related. For an excellent account of various degrees of otocephaly in the guinea pig and their relation to cyclopia the reader must be referred to a recent paper by Wright and Wagner ('34).

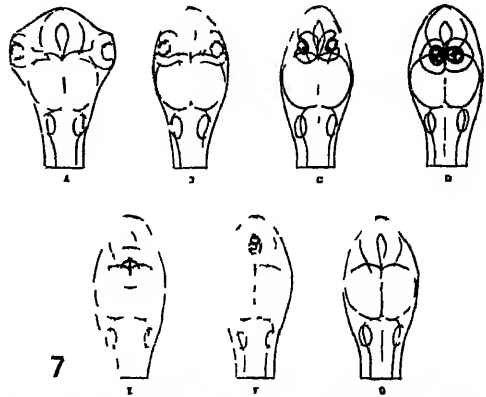


FIG. 7. DIAGRAMS (FROM STOCKARD, '09) OF THE VARIOUS DEGREES OF THE CYCLOPAN DEFECT SHOWN BY "MAGNESIUM EMBRYOS" FROM THE NORMAL A TO COMPLETE ABSENCE OF THE EYES G.

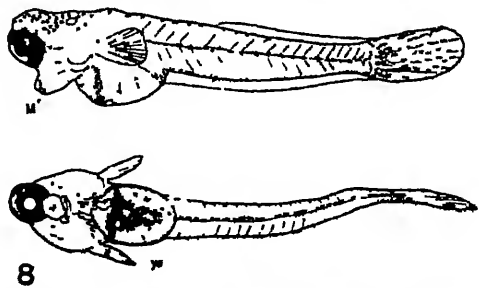


FIG. 8. LATERAL AND VENTRAL VIEWS OF A FREE-SWIMMING FUNDULUS (FROM STOCKARD, '09)

The mouth *M* is deformed, the eye perfectly single, possessing one lens and one pupil.

Between the perfect cyclopean and the normal condition a complete series of intermediate conditions may be recognized (fig. 7). Increasing degrees of doubleness of the eyes tend to be accompanied by increasingly normal conditions on the part of the other organs of the prechordal region of the head. Kundrat ('82), Fischel ('21), Adelman ('34) and

others have pointed out the fact that the degree of malformation of the brain tends to parallel closely the degree of approximation of the eyes. However, cerebral anomalies are not always accompanied by cyclopia (Wright and Wagner, '34).

Aside from the complex of anomalies above described, which constitute an essentially integral part of the cyclopean condition, a number of other abnormalities, which are obviously not causally related to it, have been reported as occurring in connection with cyclopia. They include among others, hare-lip, spina bifida, umbilical hernia, situs inversus of the viscera and uterus unicornis. More extended lists with appropriate references to the literature may be found in Ballantyne ('04), Ognew ('30), and Wright and Wagner ('34).

The single median eye of cyclopia perfecta may vary considerably in size, being often somewhat larger than a normal eye, often smaller but normally formed, and sometimes rudimentary and abortive, being sometimes represented by only a tapetal sac. This latter condition is but a step removed from one characterized by complete absence of the eye (Anophthalmia mediana). With asymmetrical forms, exhibiting unilateral microphthalmia or suppression of the eye, we are not primarily concerned.

A number of authors have endeavored to establish satisfactory classifications of cyclopean and related monsters (Vrolik, '49; Geoffroy St. Hilaire, '32-'37; Bock, '89; Blanc, '95). These are conveniently summarized by Schwalbe and Josephy ('13), but due to the fact that cyclopia and various associated anomalies often intergrade, none has been universally adopted. We follow Mangold ('31) in adopting the simple classification of Werber ('15), distinguishing six degrees, (1) Synophthalmia bilentica, (2) synophthal-

mia unilentica, (3) cyclopia synophthalmia, (4) cyclopia perfecta (monophthalmia mediana), (5) microphthalmia mediana, (6) Anophthalmia mediana (see fig. 7).

#### *Relative Frequency of Cyclopia*

Little can be said concerning the relative frequency of cyclopia in the various vertebrate species. It has been observed and described more frequently in man and the pig (Schwalbe and Josephy, '13, p. 210) than in other forms, which is perhaps only natural; but obviously a survey of the cases described in the literature can yield no reliable figures as to the absolute or relative incidence of the anomaly. The figures would merely indicate in a general way the relative frequency of opportunity to observe the anomaly. Such is obviously the case in the compilation of Hannover ('82) where of 268 cases, there were 103 human foetuses, 130 pig, 51 lamb, 22 dog, 12 cat, 10 horse, 9 goat, 3 rabbit, and 1 deer foetus. Somewhat more significant figures, derived from Panum ('60), are given by Mall ('08) for man; in a group of 618 human monsters, 16 were cyclopic and 9 anophthalmic. In Mall's own cases, three of forty-eight embryos had "misplaced eyes". The figures of Wright and Eaton ('23) reveal a .2 per cent incidence of otocephalic monsters (cyclopean included) among about 40,000 guineapigs; in one branch of this strain the percentage ran about 27 per cent. However the figure for cyclopia would be only a fraction of the above figures.

#### *Viability of Cyclopean Monsters*

Human cyclopean monsters, as a general rule, survive, if at all, for only a few hours after birth. Von Hippel ('00) records one, however, which is said to have lived ten years! The severity of the anomaly in this case is not stated. Whether the

abnormality of the brain, in higher forms at least, is responsible for their speedy demise, is uncertain. In fishes, amphibia and other yolk-rich forms, they are able to survive in almost every instance only as long as a supply of yolk remains, for the mouth is almost invariably imperfect. Stockard states that many *Fundulus* embryos showing a cyclopean defect hatched normally, were able to perform normal swimming movements and gave indications of ability to see. In some instances they lived for over a month (Stockard, '10a). Paolucci ('74), however, described a cyclopean ray (fig. 3), caught in the Adriatic, which measured 20 cm. to the base of the caudal fin. The mouth was well-formed and any brain anomalies (not described) which may have existed were apparently relatively unimportant as far as the animal's ability to survive so long was concerned.

## II. EXPERIMENTAL PRODUCTION OF CYCLOPEAN MONSTERS

The hope of one day attaining an adequate understanding of cyclopia is considerably strengthened by two important considerations, first the fact that the anomaly may be experimentally produced with considerable ease, and secondly, the fact that experimentally produced cyclopean monsters exhibit essentially the same features as those 'spontaneously' arising.

Aside from some preliminary experiments of Geoffroy St. Hilaire's, Dareste ('77) was the first to undertake systematically the experimental production of developmental anomalies. By incubating eggs in a vertical position, the use of abnormal temperatures, varnishing the shell with substances impermeable to air, and unequal warming of the eggs, he was able to produce "several thousand" monstrous chicks, among which were some

exhibiting various degrees of cyclopia. Féré ('00, p. 796) also obtained cyclopean chicks from eggs subjected to relatively high temperatures before incubation. *Fundulus* eggs reared for a short time after fertilization in subnormal temperatures may also give rise to cyclopean monsters or other eye defects (Kellicott, '16; Loeb, '15).

The production of cyclopia by the use of chemicals has been highly successful. This was first accomplished by Stockard ('07-'10) in his now classical experiments on *Fundulus* embryos treated with varied strengths of  $MgCl_2$ ,  $MgCl_2 + NaCl$ ,  $Mg(NO_3)_2$ , and  $Mg(NO_3)_2 + NaCl$ . Alcohol, ether, chloroform and chloretone were also used, alcohol being most effective; at times as many as 90 per cent of the embryos treated with a 3 per cent solution were eyeless, asymmetrically monophthalmic, or cyclopean ('10a, p. 371). His experiments further show that the action of chemicals must be exerted relatively early since eggs treated later than 15 hours after fertilization failed to respond, the most effective period being the 8-32 cell stage. Cyclopean fish embryos were subsequently produced in variable numbers by the use of  $NaCl$ ,  $LiCl$ ,  $NaOH$ , amyl alcohol, acetone (McClendon, '12a), and butyric alcohol (Werber, '16a, b).

Cyclopean amphibian embryos have been produced by treating the eggs in early stages of gastrulation with lithium chloride, ethyl alcohol, chloralhydrate (*Rana*, *Triton*, LePlat, '13, '14, '19; *Rana* and *Triton*, Cotronei, '22a, b; *Rana*, Guareschi, '34; *Amblystoma*, Adelman, '34), phenol and chloretone (*Triton*, Lehmann, '33). The exposure of incubating eggs of the fowl to alcohol vapors is productive of a small percentage of cyclopean monsters (Féré, '99; Stockard, '14).

Cyclopia has also been produced by mechanical interference. The experiments of Spemann ('01 b, '02, '03 a, '04) are of special interest in this connection. By constricting the egg of *Triton* with a hair loop in stages ranging from the two-cell to early gastrulation stages, double headed monsters were produced (fig. 9). If the ligature was oblique, the component related to the smaller segment of the blastopore was small and often cyclopic. When the constriction was less pronounced

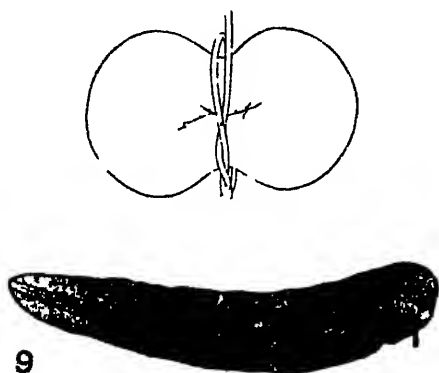


FIG. 9. LARVA OF *TRITON TAENIATUS* (BELOW) ELEVEN DAYS AFTER OBLIQUE CONSTRICTION OF THE EARLY GASTRULA (ABOVE)

The constriction of the gastrula results in incomplete doubling of the head of the larva, the left side of which is normal, the right cyclopean. Only the right eye of the left head can be seen in the figure. On the right side the single cyclopean eye, the single olfactory pit lying above it and the closely approximated balancers are shown. (From Spemann, '04).

three-eyed monsters might result, the middle eye being shared by the two incompletely separated heads and one case of partial fusion of four eyes is described. By pricking the anterior end of the embryonic shield of *Fundulus*, Lewis ('09) obtained some typical cyclopean specimens. Especially interesting, however, is the experiment of Mangold ('31) who was able to produce the anomaly by the removal of the anterior portion of the roof of the archenteron of *Triton*. (Fig. 10).

#### *Attempts to 'Explain' Cyclopia*

The greatest diversity of opinion has existed as to the cause of cyclopia. This is, no doubt, partly due to the failure on the part of some to appreciate the fact that a number of very diverse factors may evoke essentially the same morphogenetic response; partly to an imperfect knowledge of the exact nature of the physico-chemical or mechanical alterations of cells produced by alteration of environmental conditions and their expression in morphogenetic terms; and also, in large part, to the incompleteness of our knowledge of normal developmental processes, a condition which has now been, at least partially, remedied by experimental work, notably by Spemann and his school.

We may at once eliminate maternal impressions from the list of possible 'causes' which have been advanced to account for the anomaly. Dareste ('77, '91) and others have regarded cyclopia as due to amniotic compression leading to an arrest in the development of the anterior cerebral vesicle. Although there is evidence that the anomalous formation of the amnion, dating from the earliest stages of development, is sometimes associated with malformations (Streeter, '30), the fact that cyclopia is common among the anamniota and that no confirmatory evidence of its rôle in the production of the anomaly in the amniota exists, indicates that we may eliminate this factor, also, as a causative agent, at least in the vast majority of cases.

#### *The Nature of the Action of Physical and Chemical Agents*

We are still ignorant of the exact nature of the effects of chemical and thermal alterations of the environment. Stockard ('10a) at first believed that eye anomalies "all of which are more or less arrested

conditions of development, result from anaesthesia during development", but McClendon ('12a) obtained similar results with NaCl, LiCl, and NaOH "to which an opposite effect is rather to be ascribed". Finding the order of effectiveness of kat-

of different substances. Werber ('16a, b) believes that various solutions produce a chemical lesion (Blastolysis) so altering the cells chemically as to render those affected incapable of the reactions necessary for normal development. LePlat

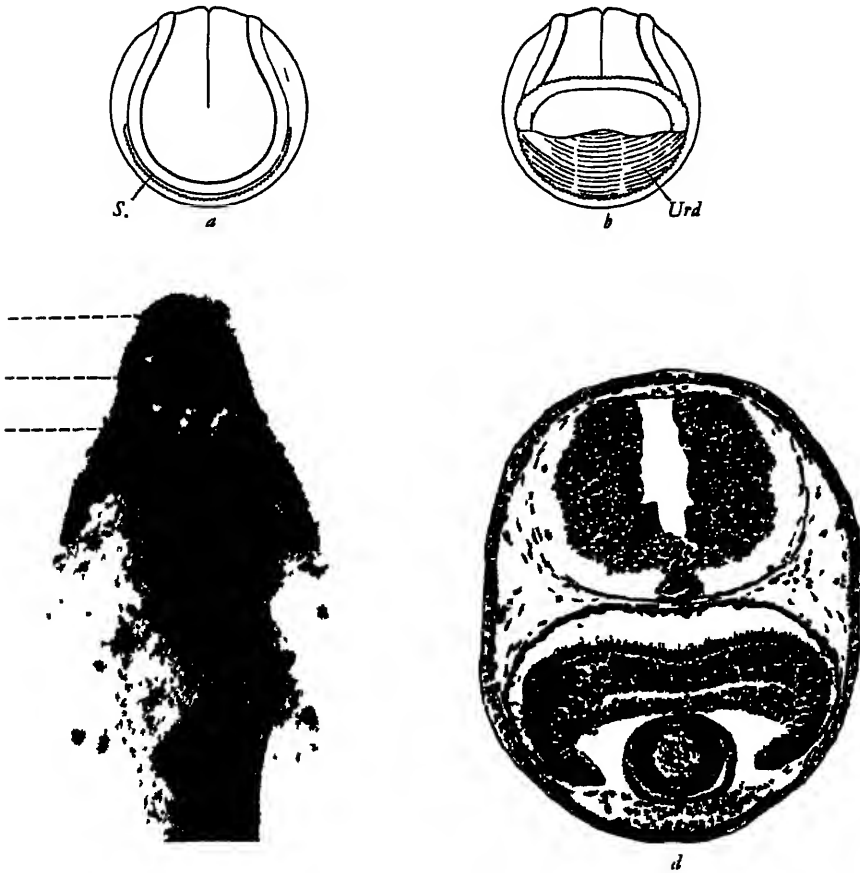


FIG. 10. PRODUCTION OF SYNOPHTHALMIA AND CYCLOPIA IN THE EARLY NEURULA OF TRITON

Figures *a* and *b* are schemas showing the operation which consists of cutting around the cephalic fourth of the medullary plate peripheral to the neural ridge, flapping back the medullary plate, and removing the underlying roof of the archenteron. Figure *c* shows the embryo ten days after the operation. Figure *d* is a section through the head showing an almost completely single eye with a single lens. (From Mangold, '31.)

ions in producing cyclopia to be  $Mg < Li < Na$ , he supposed their action to be physico-chemical. The degree of toxicity (McClendon, '12b) is apparently not important, solutions of equal toxicity showing striking differences in the effects

('19) in his judicious summary of the subject concludes that "there is no specific teratogenetic substance, that numerous toxic agents modify development, very probably by action on the nuclei, and that it is the stage during which the agent

has actively influenced the development of the egg which has provoked the differences in the observed results". The same solutions produce a graded series of anomalies. Thus, a .5 per cent solution of  $\text{LiCl}_2$  acting upon young blastulae of *Rana* results in abnormal gastrulae with largely open blastopores. In the early stages of gastrulation it produces asyntaxia medullaris, cauda bifida, anencephaly, anophthalmia, rudimentary brains, nanism, hydrops and paralysis. Acting upon more advanced gastrulae cyclopia is the most commonly observed anomaly, while later on the embryo grows incapable of withstanding such marked changes in environment and dies.

As to the observable effects of low temperatures Kellicott ('16) states that they consist in inequality in the distribution and combinations of both nuclear and cytoplasmic substances, and in disturbances in the formation of the cell walls. "The cause of abnormal and monstrous development . . . is to be found in a disturbance of the normal organization of the ovum."

The evidence as a whole, therefore, seems to indicate that there is no specific agent responsible for the production of cyclopia, that a variety of abnormal environmental influences may produce a graded series of abnormalities depending upon the severity of their action, the time of development during which they act and the vigor of the individual. All things considered, the most active tissue at the time will be most seriously affected, and upon what parts of the embryo are affected will depend the subsequent course of development as a result of the initiation of a series of abnormal developmental interactions. This, in a general way, is in conformity with the theory of differential susceptibility advanced by Child ('20, '21, '28) in connection with the

theory of axial gradients. Any specificity which exists will, therefore, as LePlat ('19) and Stockard ('21) point out, be related rather to the period of development during which the inhibitory agent exerts its influence than to any specific action of the same. For a more thorough review of the evidence concerning these so-called critical periods of development, the work of Needham ('31) should be consulted.

In the same general category belongs Mall's ('08, '17) theory that nutritional disturbances, occasioned, in the case of placental forms, by faulty implantation, are responsible for anomalous development.

#### *The Rôle of Genetic Factors*

Defects of the germ plasm have also been held to be a possible agent, notably by Wilder ('08) and there is evidence to show that this may be true in some cases, although the evidence seems to indicate that in most instances environmental, rather than hereditary factors, are responsible (Stockard, '10). In this connection we may note that cyclopia has been recorded as occurring in siblings (van Duyse, '09; Klopstock, '21; Mall, '17) but we must recognize that a germinal origin is not thereby proved since we are ignorant of environmental conditions obtaining in the uterus. However, that germinal factors may sometimes be involved is clear from the work of Loeb ('15) who was able by hybridization to produce eye defects in *Fundulus*. Further evidence is adduced by Wright and Wagner ('34) who have studied a series of over 300 monstrous guinea pigs descended by brother-sister mating from a single mating made in 1906. Most of these are otocephalic and many are, in addition, cyclopic. They conclude that both environmental and hereditary factors take part and sug-

gest that the latter are the ones which bring about a general inhibition to which the momentarily most active regions of the embryo are susceptible. "Whether the genes have a directly depressive action at the critical moment or whether they produce such an increase in activity as to bring about susceptibility to trivial environmental conditions is a question to which no answer can be given at present."

#### *Morphogenetic Interpretations*

On the morphogenetic side most of the attempts to explain cyclopia have centered in the interpretation of the origin and nature of the early eye anlagen. Speer (1819) and Meckel (1826) interpreted the anomaly as due to the more or less perfect fusion of two originally separate eyes and the concomitant malformations of the head were likewise interpreted on the basis of simple fusion of separate parts. On the other hand, Huschke (1832) from his study of the early development of the chick concluded that the two eyes are represented early in development by a single vesicle situated anterior to the brain which subsequently grows forward to effect a subdivision of the originally single optic anlage into two optic vesicles. Cyclopia was interpreted as a developmental arrest. Some external factor operating early in development was thought to simultaneously inhibit the further evolution of the brain and eye, and these in turn when they remained single would constitute the causal factor for associated malformations of the skeleton and musculature.

It may be stated at once that in its original form neither of these explanations is any longer tenable. While more or less complete fusion of optic cups or vesicles has been experimentally effected (Born, '97, pp. 537 ff.; Anastasi, '13; Pasquini,

1927a, p. 74, 1927b, 1929a, p. 100, 1929b, p. 264; Truniger, '27; Detwiler, '29) modern workers are agreed that no crude fusion of already formed optic vesicles can be demonstrated as occurring, at least in experimental cyclopia (Spemann, '04, '12b; Stockard, '09b). Huschke, as Dareste ('77) points out, obviously confused the entire prosencephalon with the optic vesicles which are in all vertebrates normally paired when they first push out from the walls of the forebrain, a fact clearly established by von Baer (1828, pp. 23-24). It is interesting to note, however, that von Kupffer's ('90) description of an originally single optic vesicle in *Petromyzon* was only recently refuted by Keibel ('28).

Although discredited in their original form, the interpretations of Meckel and Huschke survive in altered form in two opposing points of view of more modern workers. The fact that the cyclopean eye is single from its first appearance does not preclude the possible fusion of two prospective anlagen in earlier stages of development, nor the possibility of a primitive potentially single anlage which subsequently becomes separated into two parts with the expansion of the optic vesicles. This furnishes the basis for two opposing schools of thought at the present time.

Dareste ('77, '91) advocated the fusion of separate optic anlagen attendant upon a developmental arrest which delayed the closure of the anterior neuropore and inhibited the forward growth and bilateral expansion of the prosencephalon. The parts destined to form the optic vesicles consequently fuse and form a single evagination anterior to the foregut. Pressure of the amnion was supposed to be the inciting factor.

Spemann is the leading contemporary advocate of this view that two separate



and distinct optic anlagen are normally determined in the early neural plate. His thoughtfully conceived and beautifully executed experiments on *Rana*, *Bombinator* and *Triton* (Spemann, '01b, '03a, '04, '12b) have convinced him that there exists in the early neural plate stage a complete and rigidly determined mosaic of all the parts of the future cyclopean or normal

its prospective significance when transplanted (Spemann, '12a) or displaced by rotation of a rectangular area of the anterior end of the neural plate (Spemann, '12b). This experiment (fig. 11) consisted in the rotation through 180° of a rectangular area of the anterior end of the neural plate together with the underlying roof of the archenteron. If the anterior

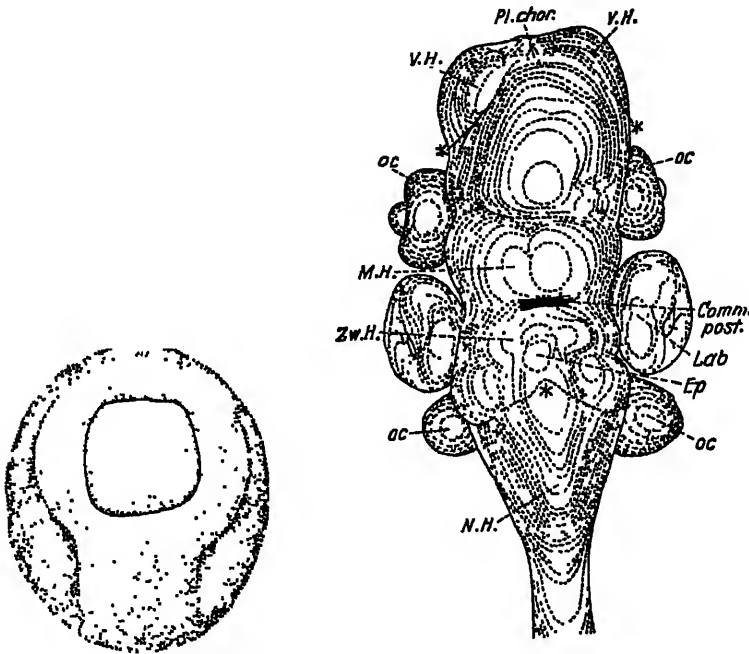


FIG. 11. ANTERO-POSTERIOR ROTATION OF A PIECE OF THE MEDULLARY PLATE TOGETHER WITH THE UNDERLYING ROOF OF THE ARCHENTERON

Figure *a* shows the experiment. Figure *b* shows a reconstruction of the brain and eyes ten days after the operation. *Comm. post.*, posterior commissure, *Ep.*, epiphysis; *Lab.*, labyrinth, *M.H.*, midbrain; *N.H.*, hindbrain; *oc.*, optic cup; *Pl. Chor.*, choroid plexus, *V.H.*, forebrain; *Zw.H.*, diencephalon. The line marked with an asterisk shows the line of fusion. (From Mangold, '28, after Spemann, '12b).

eye. The visual and pigment layers of the retina, the optic stalk and chiasma all occupy definite areas of the neural plate and are unable to substitute for one another when one or the other is rendered defective or is lacking, as after puncture of the anterior end of the neural plate with a hot needle (Spemann, '01a, '03b). Each differentiates strictly in accordance with

end of the excised piece passed through the eye anlagen, four eyes were developed in the embryo after healing, two from those portions of the optic mosaic remaining in situ and two from the caudally displaced portions. The right posterior and left anterior eyes, and vice versa, supplemented one another qualitatively and quantitatively, the parts lacking or

underdeveloped in one being represented in the other. A caudally displaced tapetal vesicle was for example matched by a well developed eye formed on the opposite side in its normal location. As a result of his constriction experiments, previously referred to, he concluded that the cyclopean eye is likewise represented in the neural plate by a mosaic of rigidly determined parts, in this case the single median primordium having arisen by the fusion of more laterally situated parts due to the absence or deficiency of median regions of the neural plate. Fischel ('21) has adopted Spemann's conception in his study of cyclopean *Salamandra* embryos and attempted to reconstruct the arrangement in the neural plate of the parts of the optic mosaic of both normal and cyclopean eyes by following back into it the various parts of the optic cup. His diagrams (fig. 12) illustrate the essential features of this point of view which has received further experimental support from King ('05) and from Lewis ('07, '09) who was able to produce typical cyclopia in *Fundulus* by injury of the anterior end of the neural plate with a heated needle. It has also been adopted by many subsequent writers (e.g. Mall, '17; Seefelder, '08, '30; Cotronei, '22; Tsuda, '24; v. Querner, '25; *et al.*).

The opposing view that the two eyes are represented in the neural plate by a single median zone of eye-forming material finds its champion in Stockard, who as the result of his studies on cyclopean *Fundulus* monsters (Stockard, '09b) and excision experiments on *Amblystoma* (Stockard, '13a, b) concluded that the

eye anlage in the medullary plate is primarily median and single and normally separates into two almost equal growth regions which develop in lateral directions reaching further and further out until finally the optic vesicles come into contact with the ectoderm ('13b, p. 254). There is no medullary material between the eye anlagen. The median tissue is the

eye anlage itself and will subsequently go to form some portion of the eye, either optic cup or optic stalk, depending upon its position and the extent of normal development attained (p. 269). In . . . cyclopia . . . the median eye anlage does not widen or spread laterally but is arrested in its primary condition, thus the two growth centers are not sufficiently separated and only a single optic center exists . . . (p. 273).

Essentially similar to Stockard's interpretation is that of LePlat ('19) who introduced the convenient term "optico-ocular apparatus" which includes all of the structures—the optic vesicles, optic stalks and primary optic chiasma—which develop from the "simple median anlage precociously formed in the medullary plate" (fig. 13).

A third interpretation has been developed by Rabaud ('01, '02) who studied a large number of cyclopean chick embryos. His position is difficult to understand but in essence he maintains that the developmental processes underlying the formation of the cyclopean head have no analogy in normal development. The neural plate remains flat for a long time and is subsequently closed by a sort of epiboly of the cells at its margins. The simple cyclopean eye arises not by a fusion of separate anlagen but as a result of a more or less complete "indivision" of a common anlage. His interpretation in this latter respect is therefore somewhat closely related to that of Stockard. As Schwalbe and Josephy ('13, p. 245) point out it is likely that Rabaud was dealing with anencephaly rather than cyclopia proper for no comparable delay in the closure of the neural folds has been described in other forms.

It will be clear that, aside from the possibility that the cyclopean eye is a structure arising by processes finding no parallel in normal development, its explanation in morphogenetic terms will depend upon whether the first or second

of the above interpretations is accepted. If the optic anlagen are regarded as double and separated by medullary tissue, the

the eyes is present in the neural plate as a median group of cells which subsequently spreads laterally to give rise to two eyes,

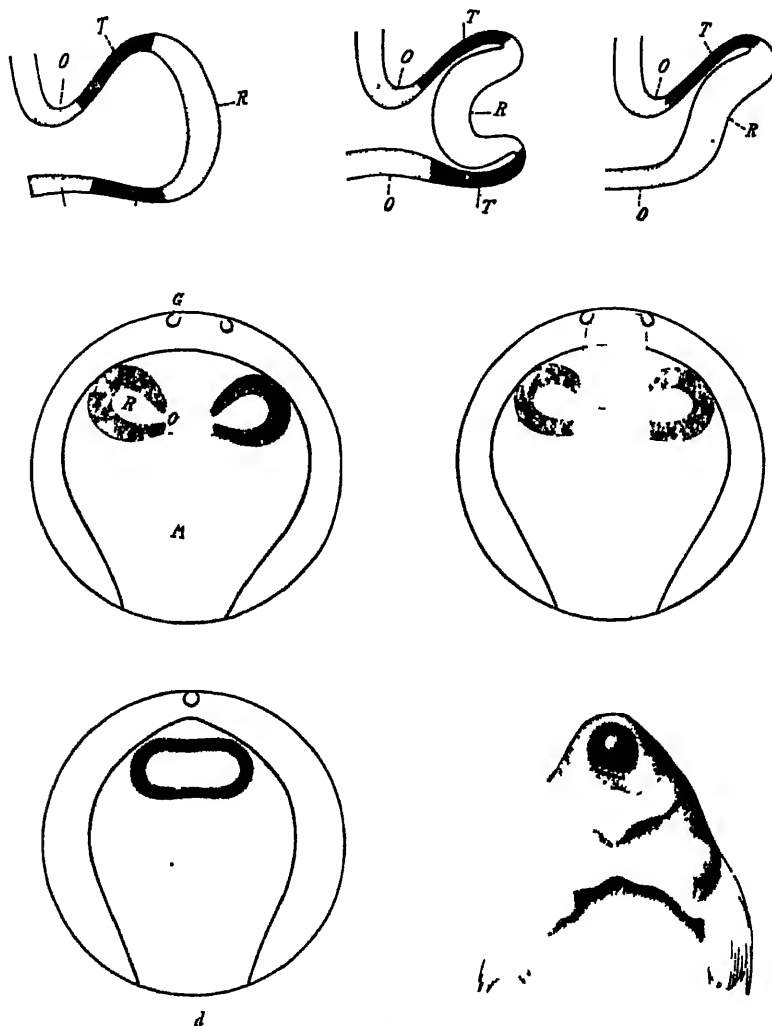


FIG. 12. (A) THE NORMAL TOPOGRAPHY OF THE EYE-FORMING MATERIALS OF THE NEURAL PLATE ACCORDING TO FISCHER ('21). (B) SCHEMATIC TRANSECTIONS OF THE NORMAL OPTIC VESICLE AND CUP, SHOWING THE UTILIZATION OF THE REGIONS MAPPED OUT IN (A). (C) DIAGRAM SHOWING THE EXTENT OF THE MEDIAN 'DEFECT' IN CYCLOPIA PERFECTA. (D) THE ARRANGEMENT OF EYE-FORMING MATERIALS IN CYCLOPIA PERFECTA. (E) VENTRAL VIEW OF HEAD OF LARVA OF SALAMANDRA ATRA EXHIBITING CYCLOPIA PERFECTA. (FROM FISCHER, '21).

G., olfactory pit; M., medullary plate; O., optic stalk; R., retina; T., pigment layer of retina.

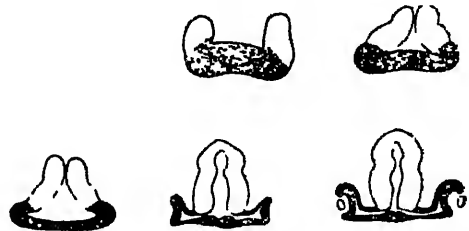
cyclopean eye can arise only when the median region is defective or lacking. On the other hand, if the material for

cyclopia will be interpreted as an arrest in eye formation. The median group of eye-forming cells in case its bilateral

expansion is checked must be thought capable of differentiating harmoniously into a single cyclopean eye.

While, as we shall have occasion to point out, both interpretations have a large element of truth and the results of the experiments performed are perfectly valid under the conditions imposed, later work has served to show that a reinterpretation is probably necessary. A number of objections to each in its original form immediately come to mind. (1) Thus in attempting to schematize the Spemann interpretation Fischel ('21) has represented the materials for the optic stalk and chiasma as being confined to a narrow median region of the neural plate, but Petersen ('23) has pointed out the incorrectness of this assumption. It is clear that when projected into the neural plate the material for the optic stalks would form a complete ring around the tapetum region on both sides, as illustrated in figure 14 and would not be confined to median territory as Fischel's diagrams indicate. A purely median defect would therefore not lead to an entire lack of optic stalk material and it is, moreover, difficult to conceive what circumstances would lead to a strictly localized bilateral deficiency of these rings of prospective optic stalk cells resulting in the absence of optic stalk and chiasma observed in many cases of cyclopia. (2) The fact that imperfect eyes may develop after puncture of the neural plate by a heated needle (Spemann, '01a, '03b) and that eyes lacking tapetum or retina may in some cases develop from transplanted fragments of the neural plate (Lewis, '07; Spemann, '12a) does not positively prove that the cells are not equipotential to a certain degree. Altered conditions of development (as when the eye comes to lie in the coelom) may have prevented a full expression of potencies. In some

cases possibly too small a fragment has been transplanted. There is furthermore no exact knowledge of what cells have been damaged or removed in these experiments and the lack of parts must be explained by the assumption that certain cells have been destroyed or not transplanted. (3) Recent experiments (Adelmann, '29a, b; Mangold, '31, p. 222), as will subsequently be noted, indicate that the prospective eye-forming territories are not sharply delimited in their potencies. (4) Finally the experiments performed in support of both interpretations were carried out and interpreted without



13

FIG. 13. A SERIES OF DIAGRAMS ILLUSTRATING THE CONCEPTION OF LEPLAT

The single median 'optico-ocular' anlage of the neural plate stage is represented as expanding to form both eyes and the intervening material of the floor of the brain in the region of the primitive chiasma. (From LePlat, '19).

reckoning on the influence of the roof of the archenteron which Spemann ('24, '31), Marx ('25), Mangold ('33) and other workers have subsequently shown to exercise such a profound influence on the determination not only of the eye but of the neural plate in general.

### III. THE PROSPECTIVE SIGNIFICANCE AND PROSPECTIVE POTENCIES OF THE NORMAL OPTIC ANLAGEN

It will be evident that in attempting to derive an explanation of cyclopia from the normal disposition and characteristics of the eye-forming materials of early stages, two aspects of the problem—the

prospective significance and the prospective potencies of the cell groups—should always be clearly delimited. The former is a purely morphological concept dealing with the normal fate of definite cells, cell groups or aggregates. Prospective potency is a physiological one, taking into account the adaptive or regulative capacities of cell groups. The problem of cyclopia is primarily a physiological one, involving the atypical utilization of cells or cell groups and is thus intimately concerned with the problem of prospective potency. In the Spemann interpretation prospective significance and potency are held to coincide from a period at least as early as the neural plate stage. In cyclopia the cells participate only in the formation of structures they would normally have formed. The single median eye arises through the elimination of a region normally utilized only in the formation of the optic stalks and chiasma which this region alone is able to form. In the Stockard interpretation, the prospective significance of the cell aggregates in cyclopia is different from the normal. A median group of cells normally utilized in the formation of the optic stalks or chiasma forms tapetum or retina. The potencies of these cells are therefore greater than their prospective significance, and changed conditions awaken latent potentialities not normally expressed.

Further, in speaking of determination it is necessary to be careful to define terms and state exactly the conditions under which a determination of parts is supposed to have occurred. As Harrison ('33) has so clearly pointed out "trouble begins when . . . we use the word to denote a state and ask the question whether an organ rudiment is 'determined' or not; meaning thereby whether it is so fixed as to its capacities that it can do but the one thing that it does do." It is a fact,

well known to experimental embryologists, that an isolated part tends to form a greater number and variety of structures than when left in situ (Lewis, '10; Kusche, '29, Bautzman, '29, *et al.*) and that furthermore the expression of more or less generalized potencies may be profoundly altered by secondary factors in the environment (Holtfreter, '29, '34).

### *The Eye Anlage*

Returning to the interpretation of cyclopia on an embryological basis, the first task therefore is to determine the prospective significance and the prospective potencies of the eye-forming materials of the normal embryo and the factors influencing the normal expression of these potencies. The use of vital dyes in the study of the prospective significance or fate of various regions of the egg was introduced by Goodale ('11) but the technique was greatly improved by Vogt ('25, '29) with so much success that the mapping of various regions of the egg and embryo has proceeded apace. The method of Vogt consists in brief in the application of thin pieces of agar, previously stained with Nile blue sulphate or neutral red, to the surface cells which absorb, retain and confine the stain in well localized areas. Vogt ('25, '29) has determined the site of the presumptive eye anlage in the early gastrula stage of urodeles and anura. In the former it lies in the region of the animal pole, in the latter about 40° to 50° above the equator. Vogt's method has been recently employed by Manchot ('29) and Woerdeman ('29) to study the prospective significance of the eye-forming regions of the neural plate. Their schemas, based on the results of their experiments, are reproduced in figures 15 and 16. Manchot, who used *Amblystoma tigrinum*, *Pleurodeles* and *Triton*, concluded that in the early neurula, when the

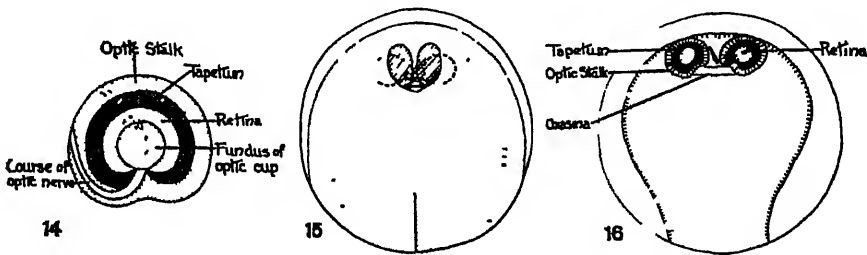
boundaries of the medullary plate are indicated by a mere pigment line, the eye anlage occupies a region corresponding in length and width to one-fourth to one-third of the greatest breadth of the neural plate, its anterior boundary encroaching upon the anterior neural ridge. During the elevation of the neural folds the eye material is drawn out and shortened in a sagittal direction and the lateral parts displaced forward somewhat so that when the neural folds have appeared, the material occupies about one-half the breadth of the neural plate and is eventually evaginated to form the optic vesicles. The materials for the two eyes are sepa-

two eye plates (Augenplatten) a group of cells which becomes the chiasma region. This expands laterally, but

that is something quite different from what Stockard thought, he assumed a median cell group in the neural plate, which grows out to both sides and separates into one anlage for the left and one for the right eye.

... In opposition to this conception, I can show that such an outgrowth does not occur, that only the territory in the midline extends in a lateral direction, but that the cell groups from which the right and left eyes arise are already in the gastrula separated from one another by material of other prospective significance

The close agreement between the schemas of Petersen ('23) and Woerdeman ('29) is at once apparent. Disregarding



FIGS. 14-16. THE SCHEMA OF PETERSEN (FIG. 14) SHOWING THE PRESUMPTIVE SIGNIFICANCE OF THE PARTS OF THE OPTIC ANLAGEN IN THE NEURAL PLATE CONTRASTED WITH THOSE OF MANHOT (FIG. 15) AND WOERDEMAN (FIG. 16) WHICH WERE CONSTRUCTED FROM OBSERVATIONS OF VITALLY STAINED EMBRYOS.

rated in the midline only by a narrow wedge of material which forms the basal portion of the lamina terminalis and chiasma. Immediately back of this wedge, continuity across the midline is effected by the materials for the optic stalk and chiasma. "If one considers the stalk material as part of the eye anlage, which according to its development appears logical, there actually exists from the first a single anlage-territory for the two eyes connected posteriorly and having an original extent closely agreeing with the statements of Stockard."

Woerdeman agrees in a general way with Manhot but insists that even in the early gastrula there lies between the

slight differences in the results of Manhot and Woerdeman, it is clear, then, that the prospective significance of a narrow median group of cells is to form the primitive chiasma region (a narrow zone in the region of the primitive optic furrow) and a part of the optic stalks. However, the question of the prospective potencies of the various portions of the eye-forming territories (optico-ocular apparatus) is still open.

#### *The Indifference of the Presumptive Ectoderm of the Early Gastrula*

In the last fifteen years much information has been added concerning the factors influencing the release or the expression of

the inherent potencies of cells and cell groups during development. Spemann ('18, '21) has demonstrated that the entire

the whole organism. Thus when the presumptive belly epidermis of *Triton cristatus* and the presumptive neural plate

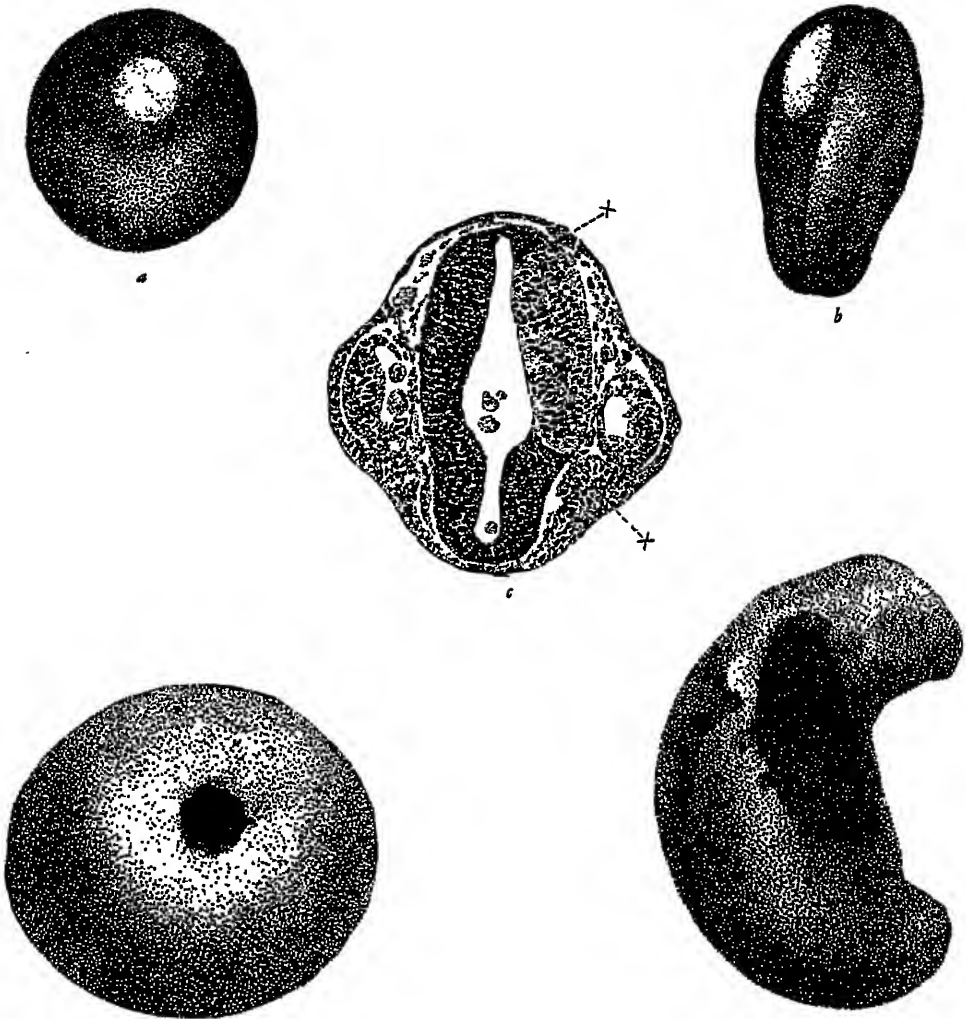


FIG. 17. EXCHANGE OF A PIECE OF PRESUMPTIVE MEDULLARY PLATE AND EPIDERMIS IN THE GASTRULA STAGES OF *TRITON TAENIATUS* (A-C) AND *TRITON CRISTATUS* (D, E).

The presumptive belly ectoderm of *cristatus* forms part of the neural plate (b) and brain (c) of *taeniatus*. The presumptive neural plate of *taeniatus* forms epidermis in *cristatus* (e). (From Mangold, '31, after Spemann).

presumptive ectoderm of the early gastrula is to a certain extent 'indifferent' or plastic and that the fate of any particular region of it depends largely upon its relations to

of *Triton taeniatus* are exchanged (fig. 17) the former, coming to lie in the anterior end of the neural plate of the host, participates in the formation of the eye and

neural tube; the latter forms epidermis. Presumptive ectoderm may, in fact, yield mesodermal structures under certain conditions (Mangold, '23). The fate of these tissues is obviously controlled by some factor, not species-specific, resident in their organismic environment. Holtfreter ('34) has recently demonstrated the same fact in an equally striking fashion. Presumptive epidermis and prospective neural plate when cultured in physiological salt solution both yield irregular masses of epidermal cells. In the early gastrula stage the entire ectoderm represents a homogeneous, harmoniously equipotential system which requires for differentiation in accordance with its presumptive significance (*herkunftsgemäss*) certain external factors not offered by this particular culture medium. When reared in a coelomic sac, however, (Holtfreter, '29) presumptive medullary plate may differentiate into typical nervous tissue. It has also been shown that in the developing organism the differentiation of the nervous system normally proceeds under the influence of the roof of the archenteron or the dorsal regions of the marginal zone of the blastula or gastrula from which it is derived (Spemann and Mangold, '24, '31; Bautzmann, '26; Marx, '25; Lehmann, '26; Mangold, '33; *et al.*). Holtfreter ('33a) has demonstrated the same effect in tissue cultures. A large piece of gastrula ectoderm of *Triton alpestris* (presumptive epidermis or medullary plate) was combined in a medium of physiological salt solution with an isolated piece from the dorsal marginal zone (presumptive roof of archenteron) of *Triton alpestris*. The pieces were broken into small fragments and mixed together. In this case, under the influence of the materials of the marginal zone which differentiates into notochord, muscular tissue and pharyngeal epithelium, the prospective ectoderm has

differentiated into neural tube. Holtfreter concludes that these induction effects obtained in explants confirm the conclusion reached by other workers that the origin of the entire nervous system and the sense organs is dependent upon its being underlain by the derivatives of the dorsal marginal zone of the gastrula. In accordance with these results it is not surprising to find that the eye anlage also depends for the localization and the expression of its potencies upon some influence exerted by the roof of the archenteron.

#### *The Localization of Eye-forming Potencies*

In attempting to determine the time when these eye-forming potencies are first localized in the region of the anterior end of the neural plate, Mangold ('28) transplanted from various species of *Triton* in different stages of gastrulation the presumptive brain and eye anlage without the roof of the archenteron into the blastocoele of young gastrulae. The youngest transplant which yielded an eye was derived from a donor with a medium sized yolk plug. It had been completely underlain by the roof of the archenteron at the time of transplantation (fig. 18). The frequency with which eyes were differentiated from the transplants increased in older stages so that Mangold concludes that before the neurula stage no definite localization of eye-forming potencies exists, a definitive localization being established only in the early neurula stage. From the experiments of Stockard ('10a), Werber ('16a, b), and Hoadley ('28) on *Fundulus*, Mangold ('31) suggests that in this form also determination of the eyes occurs during the formation of the embryonic disc and is definitive by the time the "narrow" embryonic disc has appeared. Hoadley ('26) found that in transplants of the early blastoderm of the



chick onto the chorio-allantoic membrane, the first eyes were encountered in transplants from blastoderms which possessed a broad primitive streak and which had been incubated about 4 hours before transplantation. However, the eyes differentiated from these earliest blastoderms were im-

or less fixed. Further details will be found in Mangold's ('31) exhaustive review.

We may next inquire into the nature and localization of the factors responsible for the localization (or segregation) of eye-forming potencies and their expression in the differentiated eye. Mangold ('31) suggests that the localization or segregation of eye-forming potencies may be brought about in three possible ways: (1) through the influence of the entire organism, (2) through factors arising in the anlage itself during the course of development, and (3) through factors in the neighboring regions of the egg. For a discussion of the first two possibilities for which there is some evidence the reader must, for lack of space, be referred to Mangold.

The third possibility, the influence of factors residing in neighboring parts, recalls the influence of the roof of the archenteron on the differentiation of the nervous system. From the work of Spemann ('31), Holtfreter ('32a, d). Mangold ('31), *et al.* there seems to be little doubt that the localization of eye-forming potencies normally proceeds at least largely under the influence of the prechordal region of the roof of the archenteron or the dorsal portion of the marginal zone. The latter, in early gastrula stages, lies at the dorsal lip of the blastopore and since it is the first portion of the marginal zone to be invaginated moves forward under the ectoderm until it finally comes to lie under the anterior end of the prospective neural plate. The dorsal lip of the blastopore of the early gastrula transplanted to an indifferent region of the host induces a head with normally proportioned eyes. Spemann ('31) and Holtfreter ('32a, '32c) have demonstrated in the clearest fashion a regional polarization of the materials of the marginal zone

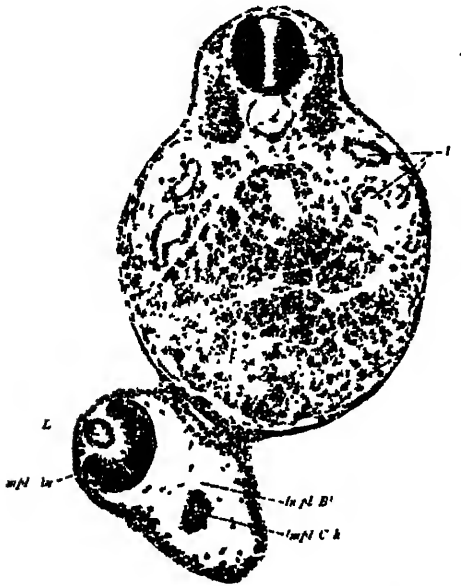


FIG. 18. SECTION OF A TRITON EMBRYO, SEVEN DAYS AFTER A PIECE OF PRESUMPTIVE BRAIN AND EYE FROM A GASTRULA OF TRITON ALPESTRIS WITH A MEDIUM-SIZED YOLK PLUG HAD BEEN TRANSPLANTED WITHOUT THE UNDERLYING ROOF OF THE ARCHENTERON INTO THE BLASTOCOELE OF THE HOST.

The implant has differentiated into a well-differentiated eye which has induced the formation of a lens. *L.*, lens, *Imp. An.*, well-differentiated eye of implant, *Impl. Bl.*, ectodermal vesicle of host evoked by the implant, *Impl. Geb.*, 'shaved' portion of implanted brain; *N.H.*, neural tube of host, *Vs.*, pronephros. (From Mangold, '28.)

perfect, a progressive improvement in the quality of differentiation occurring in transplants from later stages. The localization of eye-forming potencies in the chick evidently begins therefore during the primitive streak stage, and becomes more and more stable until the head process stage when the potencies are more

along its prospective antero-posterior axis. That a comparable qualitative difference in the inductive capacities of the roof

and described in figure 19. Further confirmation of the facts here briefly mentioned will be given subsequently.

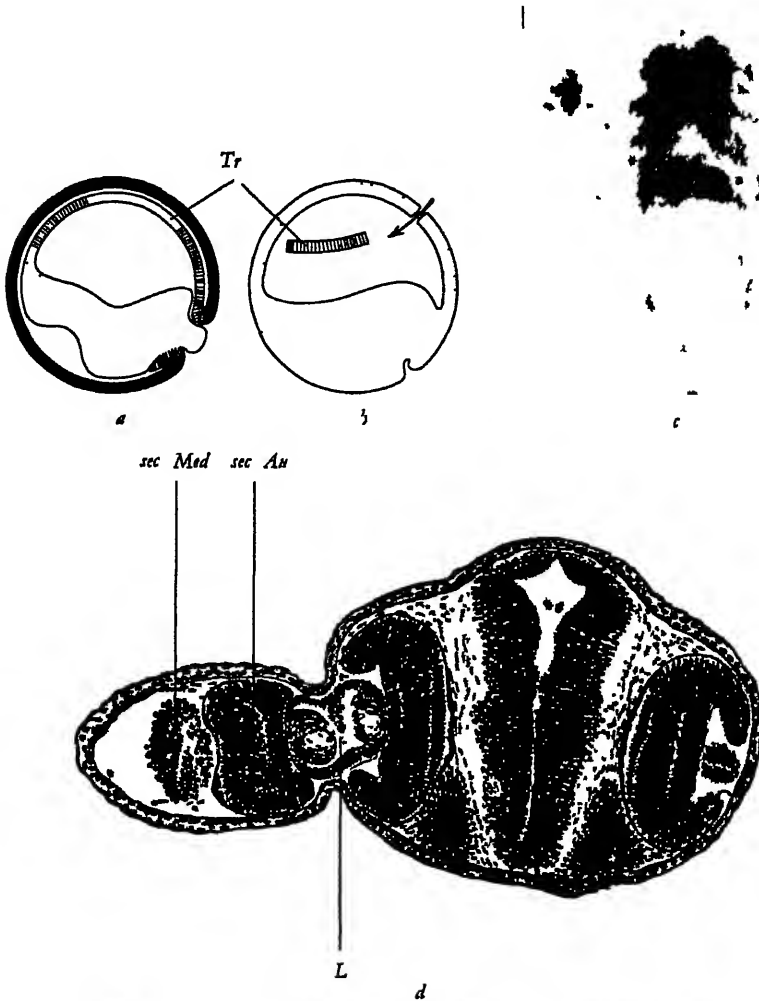


FIG. 19. THE INDUCTION OF AN EYE BY TRANSPLANTED ROOF OF THE ARCHENTERON OF TRITON

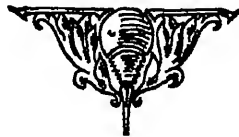
The operation is schematically shown in (a) and (b). A piece of the roof of the archenteron of a gastrula possessing a small yolk plug is implanted in the blastocoel of an earlier gastrula. (c) Ventral aspect of the host some days after the operation showing a large protuberance in the vicinity of the right eye. (d) Transsection through the head of the same. The protuberance contains a small piece of medullary tissue and a well-differentiated eye whose lens is fused with that of the host. (From Mangold '31, after Spemann).

of the archenteron exists is clear from the work of Spemann, Holtfreter, and Mangold ('33). One especially interesting experiment of Spemann's is illustrated

There is also evidence that inducing factors exist in the medullary plate itself. The transplantation of a piece of medullary plate from the presumptive eye region of a

Urodele into the blastocoele of another embryo in an early stage of gastrulation leads to the induction of a secondary brain and eye (Mangold and Spemann, '27; Mangold, '29, '29a, '32, '33). A piece of medullary fold together with some adjacent epidermis from the early neurula which would normally form some brain, olfactory placode and epidermis but no eye, may induce brain and eye when transplanted into the blastocoele (Mangold, '31). In the case of the medullary plate also a qualitative difference in its inductive capacities along its antero-posterior axis exists (Mangold, '33).

It has been possible in the preceding discussion to sketch only in the barest outline certain aspects of the induction problem, for a fuller discussion of which the reader must be referred to the voluminous literature which now exists, a guide to which is contained in the few works cited above. From what has been said, however, it will be clear that normally the localization of eye-forming potencies in the neural plate proceeds largely under the influence of the prechordal portion of the roof of the archenteron. The situation is complicated, however, by the possible action of adjuvant factors resident in the neural plate, or the 'egg as a whole'.





## MORPHOGENESIS OF THE SHOULDER ARCHITECTURE

### PART IV. REPTILIA

By A. BRAZIER HOWELL

*Department of Anatomy, Johns Hopkins University*

IN THE present contribution to the morphology of the shoulder architecture the reptilian stage will be discussed. This involves consideration of pertinent features of the skeleton of Permian and Triassic representatives of the orders Cotylosauria and Theromorpha, as well as mention of a few other fossil forms. As a basis for extended discussion of the skeleton and soft parts the lacertilian *Iguana* has been selected for the reason that live material in required quantity could be secured. Comparisons are drawn with the more significant features of *Cyclura*, and of *Uromastix* where these differ, and with the dissections of the rhynchocephalian *Sphenodon* as reported in the literature. Without live material it was thought needless to dissect the latter, as the work on it already published is of excellent quality. For the loan of both skeletal and spirit specimens of lacertilians I am indebted to the U. S. National Museum.

In any such anatomical study as the present it is necessary constantly to bear in mind the mechanics of the type of body movements employed and the position in which the parts are normally held. The modern lacertilian pose when at rest involves a right angular posture of the brachium, with elbow near the ground, and hence with the forearm directed forward. In slow locomotion the manus is advanced partly beneath the body, and the arm is then extended and retracted, with some abduction. Locomotion by primitive reptiles was doubtless much the same, except that the extent of the move-

ments was probably more restricted. In their evolution toward the Mammalia the limbs of the Reptilia underwent certain essential modifications, however. This must have included first a backward rotation of the elbow, so as to bring the manus closer to the midline during all phases of locomotor action, and finally, straightening the arm, so that the animal could stand with the minimum of fatigue. This was almost certainly a vital step in the evolution toward an active, predatory, warm-blooded mammal, and it is one that the reptiles appear to have had the greatest difficulty in encompassing. They did it, however, and the result, in change of posture, has had an important and inevitable effect in the alteration of the angle of leverage of a number of muscles. This, in turn, has accomplished modification in muscle units and in the shape of the parts of the skeleton to which they are attached.

#### SKELERON

The cleithrum was present only in some members of the Cotylosauria particularly, and of the Theromorpha, at times being vestigial in the latter; but it disappeared as a recognizable entity in Triassic times. Otherwise the clavicle and interclavicle are the only parts of the membranous girdle that survive in reptiles. The former is usually present, but is lacking in Crocodilia, Ophidia, mosasaurs and some saurians, while it is absent or vestigial in Pterosauria and Dinosauria (Williston). The interclavicle, on the whole, may be said to be at first most often

spatulate and long. Later it frequently became T-shaped and shortened, disappearing in Pterosauria, Dinosauria, chameleons, and some Plesiosauria (Williston).

It is impossible to state that *all* Permian reptiles had a suture dividing the scapular from the coracoid area, for in a few forms this is not apparent, and in some cases it disappears with advancing age. Nevertheless such a suture is characteristic of the reptiles. Most of the early forms also had a suture marking off the coracoid into two areas. This is the rule in the Cotylosauria, although it too may disappear in aged individuals. With rare exceptions among pelycosaurs this statement also applies to Theromorpha. In the Lower Permian *Varanosaurus* the part of the coracoid posterior to the suture is relatively minute, while in the related *Varanoops* this was either lost entirely or remained permanently unossified (Williston). In *Ophiacodon* its ossification was much delayed, thus suggesting a reduction (Romer). Archosaurs (theodonts, crocodiles, dinosaurs) on the whole had girdles that were quite narrow, with the coracoid undivided by suture, and this is the case in chelonians (the "procoracoid" in that group is a proscapular process). In living, lizard-like reptiles the coracoid is also undivided by a suture, but in many the surfaces are broad and the entire bony complex, including scapula, comprises in adults a single plate.

The identification of the single coracoid component in later reptiles and interpretation of the condition in mammals have involved one of the most controversial questions in morphology. To review the evidence that has been presented would require a volume, but a brief indication of the points at issue is in order.

The chief effort in the consideration of the problem of the coracoid has usually been directed toward an attempt to iden-

tify the coracoid divisions in modern reptiles and birds, monotremes, and placental mammals, but the basic arrangement in primitive reptiles is also in dispute. Of the earlier discussions it is not necessary here to speak. Some of them were excellent for the period but the consideration of evidence subsequently discovered renders obsolete many of the arguments advanced. Hence, only the more recent work will be briefly summarized. Unfortunately, individual investigators have attached such various interpretations to the terms in common use that there is much confusion now attached to them. I shall therefore, for the sake of conciseness, refer in this spot only to the three possible components of the coracoid under discussion as coracoid 1 anteriorly (for the epicoracoid), coracoid 2, and coracoid 3 posteriorly.

According to Gregory, and Hanson, in considering representation in primitive reptiles, modern reptiles, monotremes, marsupials, and placentals, coracoid 1 occurs in monotremes and fetal marsupials, coracoid 2 in all, and coracoid 3 (as well as the other two) only in primitive reptiles (but possibly vestigial in some others). This school of thought thus believes that the coracoid of modern reptiles and placentals, and the posterior division of monotremes, are homologous. Gregory was first inclined toward this belief by the discovery that in *Moschops* there was evidently a cartilaginous element anterior to the two osseous coracoids, thus suggesting that the latter completed a trio of coracoids. Accordingly he considered that fundamentally there is (a) an epicoracoid (*Sphenodon*, lizards, monotremes) dorsal to the clavicles which never reaches the glenoid; (b) the element usually termed procoracoid but which Gregory considered the coracoid, posterior to the clavicle, pierced by

the coracoid foramen, and contributing to the glenoid; and (c) a metacoracoid, contributing in early reptiles to the posterior glenoid, but lost in modern reptiles and mammals except as it may occur as a vestige. Thus Gregory considered that the posterior division of early reptiles is not found in living vertebrates. He was led to this belief largely because of the degeneracy of the posterior division (metacoracoid) in *Varanosaurus* and *Ophiodon*, and by the position of the individual divisions in respect to the glenoid.

Gregory (correspondence) has now modified his belief as expressed above—as one is constantly compelled to do in morphology—to the extent that he considers that coracoid 3 (metacoracoid) has not been lost by modern reptiles, but is represented in an undivided condition.

As opposed to this opinion of Gregory, and Hanson, it has been considered by Broom, Watson, and Romer, that coracoid 1 (epicoracoid) constitutes merely a cartilaginous margin of coracoid 2; thus that basically there are only two coracoids. They claimed that where but one representative is found it is the more cranial (coracoid 2) in modern reptiles, the more caudal (coracoid 3) in placentals (and adult marsupials), while both occur together in primitive reptiles and monotremes (and fetal marsupials). They thus believed that the single coracoid of modern reptiles is not homologous to that of placentals.

It is firmly believed that no permanent solution of the coracoid problem can be attained by using the methods heretofore followed, for there is much excellent evidence in support of both theses. An approach from another morphological angle appears to hold more promise, and some explanation of the basis for the arguments employed will be necessary.

One is prone to follow common usage,

without particular analysis, in his methods of approach to a problem. In tetrapods common usage has accustomed us to group the elements by segments, as of the brachium or carpus, although in the piscine stage all bones of the appendage were basically of the same value. The humerus is a definite entity, and we do not look upon various sutures as marking off from the humerus separable elements. We term them processes of the humerus; but they are more than mere bony prominences and their definition depends upon muscular stimuli. We think of the greater tuberosity as the prominence of the supraspinatus, infraspinatus, and teres minor muscles. In the whalebone whales the prominence of the "greater tuberosity" is determined by the deltoid muscle, however, and I think all will agree that it therefore merits a distinguishing term, for it is not the same detail as the usual greater tuberosity.

The cartilaginous girdle is just such another case as the humerus. The shoulder *element*, corresponding to the brachial element, is, however, the paraglenoid ossification. This, like the humerus, can develop processes which may become marked off by sutures, but they are extensions of the paraglenoid and not separate elements. The segment has been much affected, in what manner one cannot be sure, by the contiguous membranous girdle, with which it fuses, but at least comparative anatomy indicates that the growth from the paraglenoid region has been in three directions—dorsally, cranially, and ventrally. In such an animal as *Bryops* this consists of an expanse of bone without sutures, which is generally known as the scapulocoracoid. This is a justifiable term, the "scapula" being the part of the area giving rise to dorsal muscles, and the "coracoid" to ventral or flexor muscles. In Lower Permian cotylo-

saurs these two areas of the paraglenoid came to be marked off from one another by a suture, which passed through the glenoid. We know exactly which areas lie on either side of this suture, and that its absence does not indicate the disappearance of either scapula or coracoid areas. Similarly with the ventral division. The coracoid part of the girdle may in turn have a suture marking it off into two areas, and the position of this suture can vary.

As already indicated, we know little of the reason for sutures. Presumably they indicate separate centers of ossification, and the more distinct they are the more advanced the age, by and large, at which they disappear. Presumably also they are associated with areas of muscle stress, as well as other obscure things. Usually they mark areas of distinct muscle groups, although a division of one muscle group can easily invade the territory of a neighbor. Where a small area, as an epiphysis, is separated by suture it usually indicates a purely local stress, as the attachment of a single strong tendon. But one cannot say why sutures are present in some instances and are absent in others. At least it is certain that the absence of a suture does *not* mean that a part of the girdle is absent, but merely that it is undefined by suture.

The reason why the borders of some broad bones remain cartilaginous is also obscure. Such cartilages are prone to develop where there is attachment to other elements, as upon the sternal border of the coracoid. The muscles attached to them are almost invariably very broad ones. They might well indicate disappearing elements, but seldom can be interpreted in this light. It seems that the only safe course to follow is to call them, in the present case, the unossified portion of the dorsal, cranial and ventral

borders of the girdle, their extent contracting or expanding locally as different stimuli are encountered. In such diverse forms as *Heloderma* and *Uroplatus* cartilage remains only upon the dorsal and ventral borders, disappearing between, but in *Iguana* the cartilage is continuous upon three sides, narrow upon the sternal border of the coracoid and enormously expanded dorsally to form the suprascapula. With age the latter calcifies completely, while calcification of the remaining part is complete only here and there.

In old individuals of *Iguana* the ossified part of the girdle occurs as a single plate, without sutures. It is expanded in supraglenoid, preglenoid, and infraglenoid directions, the latter having a pronounced posterior process which extends caudal to the level of the glenoid. Directly cranial to the glenoid is the coracoid foramen. Distinctive features are the four fenestrae, bounded on three sides by bone and on the fourth by cartilage. The number of fenestrae may be significant, but not their mere occurrence. They are covered by membrane, from which muscle fibers may arise. Their occurrence is probably possible only where the localized muscle stress is not strong.

Clavicles are well developed in *Iguana*, attached dorsally to the anterior part of the suprascapula where this adjoins the scapula, and ventrally to the interclavicle. The latter is T-shaped, with processes diverging midway between clavicle and the body of the interclavicle. This is situated between the two halves of the girdle anteriorly, and between the two halves of the sternum posteriorly.

When we come to examine the skeleton of a subadult *Iguana* it is seen that the girdle does have a suture, running from the glenoid to the lower border of the second fenestration. Above the line of this suture, then, is the scapula and supra-

scapula, and virtually all of the two upper fenestrations, while below lies the coracoid portion of the girdle surrounding the two lower fenestrations. Let us examine the muscular significance of these facts.

It is clear that in modern reptiles the suprascapula is the skeletal division concerned with the suprazonal muscle group, for all of these muscles insert upon it and nowhere else. Hence it is permissible to assume that in *Iguana* the great development of the suprascapula is correlated with the exigencies of these muscles. It has an additional stimulus, however, for the disappearance of the cleithrum has allowed *m. dorsalis scapulae* to settle upon the suprascapula. Presumably the latter muscle has increased its function, inasmuch as it has encroached upon the clavicle also. It covers the dorsal fenestration of the scapula.

The chief function of the scapula is probably as a brace for the suprascapula and clavicle. It now constitutes in reptiles the girdle division concerned with those axillary muscles which have left the membranous girdle. These comprise *mm. subscapularis* and *scapulohumeralis*, the latter arising partly from the anterior cartilage of the scapula. The remaining axillary muscle, the deltoid, still arises from the clavicle, as originally. Where there is no clavicle, as in *Caudata*, the deltoid has settled upon the girdle and may build out a considerable process, erroneously termed procoracoid process. This, in reality, is the homologue of the acromial process of *Salientia*, as suggested by Anthony and Vallois, with which the deltoid has become associated after having left the clavicle, and appears to have its counterpart in the *Chelonina*, although I have not analyzed conditions in that order and cannot be sure. The term procoracoid in this connection is misleading and extremely objectionable, for it is asso-

ciated with axillary muscles of the same group as those arising from the scapula, and for it should be substituted the name proscapular process. Its only representative in the *Mammalia* is the acromion. This completes the dorsal or extensor division of the girdle.

The ventral division of the girdle, from which basically flexor muscles alone arise, is the coracoid portion. Concerned

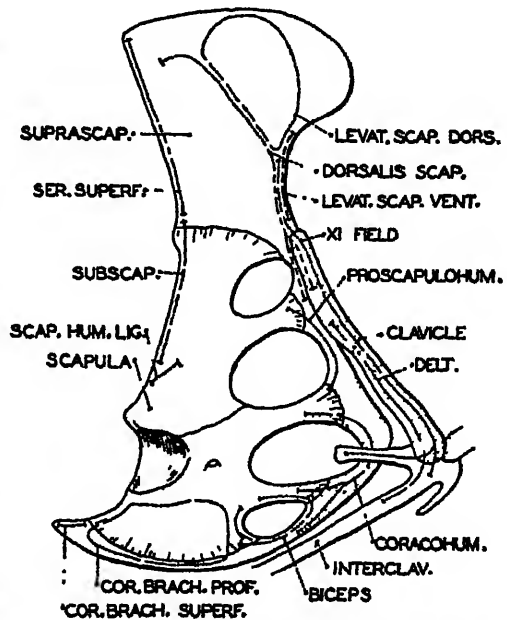


FIG. 1. LATERAL VIEW OF RIGHT SHOULDER GIRDLE OF *IGUANA*, SHOWING MUSCLE ATTACHMENTS. Clavicle and area of origin of anterior coracoid muscle matrix stippled.

with the coracoid are two distinctive muscle groups, the coracohumeral or supracoracoid matrix, and the coracobrachial matrix. Slips of these can readily be differentiated by their nerve supply. The area of bone from which arises the coracohumeral group may be called the anterior coracoid, and the part giving rise to the coracobrachial group the posterior coracoid. In *Iguana* the muscle concerned with the anterior coracoid is the single



coracohumeralis, which covers the third fenestration of the girdle and has extended ventrally so as to cover a small part of the fourth fenestration. In addition, a few fibers of this matrix have become secondarily fused with the origin of m. coracobrachialis profundus, to this extent encroaching upon the posterior coracoid area (not indicated in fig. 1).

In *Iguana* the posterior coracoid is the area of the girdle from which arise the slips of the coracobrachial matrix, covering the inferior or fourth fenestration and the part of the bone posterior thereto. Presumably in order to give a more favorable angle of leverage to some of these muscles the coracoid has developed a bold posterior process. Two areas of the coracoid are accordingly present in this genus, as well as other living, limbed reptiles. In *Iguana* they are unseparated by a suture, presumably because the two groups of muscles act largely in continuity, and not in sharply differentiated manner, as well probably as for other obscure reasons.

In the above discussion no account has been taken of m. subcoracoideus because it has so clearly invaded the otherwise unoccupied territory of the medial girdle from the axillary matrix. It is thus a dorsal division that has spread over the province of the ventral musculature, just as the ventrally derived suprascapular musculature in mammals has invaded the territory of the dorsal musculature.

It will be noted (fig. 1) that in *Iguana* there is a considerable area of the coracoid from which no muscle arises. This may be considered in this case as a sort of no-mans-land. At least one cannot decide whether it belongs more properly with the anterior or posterior division. If a suture appeared between the two areas it might run in a vertical direction through the fenestra, thus excluding the anterior

coracoid from the glenoid, as is the case in monotremes, or it might extend through the inferior fenestration and the glenoid, as in so many primitive reptiles. It is thus considered that the position of the coracoid suture is not of basic importance, but indicates merely the line of stress.

There is every reason for assuming that all primitive tetrapods had the above two groups of flexor muscles; therefore that fundamentally *Eryops* had an anterior and a posterior coracoid division, although these were not separately defined by a suture. When a suture appeared in cotylosaurs this did not alter the essential facts. Similarly when the suture disappeared in modern lacertilians the two areas were still present just the same. Even in Crocodilia, with narrow coracoid, muscles of the two groups arise from the bone and it represents undivided anterior and posterior coracoid areas. Furthermore, no divisions could be basically added, except as accessory epiphyses. There appears no more reason for recognizing the anterior cartilage of *Moschops* as a separate element of the girdle than the cartilage between coracoid and sternum of *Iguana*. They are both merely cartilaginous portions of the coracoid. There is also no reason to suppose that in such a reptile as *Varanosaurus*, with relatively broad coracoid, the coracobrachial area (i.e. posterior coracoid) was reduced to the size suggested by the posterior epiphysis or cartilage. Such is a possibility, but it is more likely that it marked the origin of the tendon of m. coracobrachialis longus—not of the whole group of muscles, the remainder of which probably extended along the coracoid proper.

It is hence claimed that there are basically four areas of the cartilaginous girdle, comprising suprascapular, scapular, anterior coracoid, and posterior coracoid divisions, in conformity with the four

groups of muscles involved, and that all four were present in Permian and Triassic reptiles, irrespective of the number of sutures present, or whether or not these sutures exclude certain areas from the glenoid. Such variation is attributable to differences in muscle attachments and consequently in stresses. The posterior coracoid area could expand and the anterior contract or vice versa, within certain limits. Furthermore, some alteration in the composition of an area could occur, because of the migration of one of its muscles to an adjoining area, but as long as one of its original muscles remained the area should be considered as present, although to a modified degree. Carrying the argument still further it is claimed that all four girdle divisions are also present in living lizard-like reptiles—that there are anterior and posterior coracoid areas, not merely a single one as generally believed.

It is not possible to make the statement that all reptiles that have ever lived had two coracoid areas. So far as I can judge every tetrapod has had coracobrachial muscles originating from the girdle, so the posterior coracoid is uniformly present. In some extinct forms, however, it appears that the coracohumeral musculature had left the coracoid, and in such case the anterior coracoid area would be lacking. In such reptiles as *Dicynodon* one can be sure that an anterior coracoid area is present, because there is a suture to indicate the fact, but the acromion shows that a part of the coracohumeral musculature left the coracoid on its way to becoming the suprascapular divisions. The situation is not clear in some of the dinosaurs with very small coracoids without sutures. It is indicated that in them none of the coracohumeral musculature migrated to the scapula, but it may all have settled down upon the sternum to

act as a pectoral division, and in that case also the anterior coracoid would be lacking.

Many investigators have set great store by the position of the coracoid foramen. Thus Gregory used it in part to identify what he termed the coracoid proper of the ventral plate. Such foramina may exhibit much conservatism, while again they migrate, in accordance with the position of the nerve concerned. The fact that the partial homologue of the coracoid foramen is represented in mammals by the suprascapular notch shows that this is an untrustworthy criterion for identifying bony areas.

It seems to have been the rule in cotylosaurs and pelycosaurs of the Lower Permian for the clavicle to have been fused to the girdle throughout its length, and under this condition no acromial process could well exist. As soon, however, as the ventral end of the clavicle became loosened from the girdle, leaving the dorsal end attached, an acromion was likely to result, just as this is barely indicated in *Iguana*. Hence the acromion marks a restricted articulation of the clavicle with the girdle. In its most primitive form this was located upon the anterior border of the girdle, but in two groups of theromorphs at least—Upper Permian and Triassic dicynodonts particularly, and to a lesser extent in Triassic theriodonts—the acromion has retreated somewhat from the border, resulting in a scapular spine and space anterior thereto which was clearly occupied by a supraspinous muscle. The same course of evolution appears to have been barely initiated by later cotylosaurs, such as *Pariasaurus*.

The glenoid presents a rather graphic record of the changes that have occurred in the fore-limb in its evolution from the typically amphibian to the typically

mammalian scheme. This has been discussed many times, most thoroughly perhaps by Romer, but the present contribution would be incomplete without a résumé of conditions.

Many of the earlier Permian reptiles had a glenoid that was entirely on the lateral surface of the girdle, no part of it being situated upon the posterior border. This is an indication that the humerus was held largely parallel to the ground and essentially at a right angle to the body. The screw-shaped type of glenoid was uniformly present in both cotylosaurs and pelycosaurs, its conformation suggesting that during locomotion the distal end of the humerus must have described an ellipse through an arc of but slightly greater than 20 degrees (Romer). The brachium was thus but little more than a lever for elevating the body, this rotating for the purpose of advancing and retarding the antibrachium. The power of rotation was denied by Watson, but demonstrated by Miner to the extent of some 90 degrees in the case of *Eryops*. Rotation of the humerus was absolutely essential for the type of locomotion concerned. There is apparent in the Middle Permian a tendency for the glenoid to shift to the posterior border of the girdle, but still it pointed backward, rather than downward, and the screw-shape of articular surface is retained. The humerus must still have been held mostly parallel to the body and its degree of movement yet restricted, but at least a start had been made toward securing vertical support and getting the manus beneath the body.

In the African series of Theromorpha (dinocephalians, dicynodonts, theriodonts) the screw-shaped character of the glenoid was lost, suggesting greater latitude in the movements of the humerus, while there developed a change in the direction in which the glenoid pointed,

from backward to downward, the latter well illustrated by *Cynognathus*. In the latter the limb must have been held essentially in the mammalian position.

Changes in the shape of the coracoid accompany alteration in the inclination of the glenoid. With a glenoid on the lateral surface of the girdle an extension of the coracoid posteriorly rendered coracobrachial muscles particularly effective in retracting and flexing the brachium. This was also the case, with slight alteration in function, with a horizontal humerus pointing mostly caudally. But with a brachium held more vertically a posterior extension of the coracoid became useless and was reduced.

The humerus in the most primitive reptiles, just as in the Rhachitomi, was tetrahedral. The plane of the proximal portion was tilted from the horizontal so that the anterior part was slightly depressed. The broad surfaces of this part therefore were directed mostly dorsally and ventrally. The anterior part constituted a bold flexor, or really a protractor, process, with sundry smaller protuberances. The distal part of the humerus was also broadened, but its plane was at a right angle to the plane of the proximal portion. Its chief definition was ventrally, in the form of an even more robust flexor process. The terminations of these broad planes of bone were for the purpose of giving increased leverage to the muscles concerned; this arrangement was necessary in mammals of considerable weight employing an essentially squatting type of locomotion.

It seems clear, from the study of muscle groups and their units, that basically concerned with the cranial or protractor process of the humerus was the insertion of *m. pectoralis*, and not improbably that of the coracohumeral musculature as well, although this may originally have been

grouped more with the coracobrachial matrix. The latter was identified with the ventral expanse of the proximal humerus, while the axillary complex was associated with the dorsal expanse. The axillary insertion most anteriorly located was that of the superficial sheet—*m. dorsalis scapulae* and *deltoideus* together—and this has come to be largely associated with the protractor process also, while the most posterior division—*m. scapulo-*

bold flexor or ventral process was concerned with the origin of the antibrachial flexors, and the dorsal process with the corresponding extensors, more weakly developed. The anterior surface of this distal expanse must have been covered by the brachialis, and the posterior by the triceps.

Except for the facts that the extremities of the bone have been separated by the development of a slender shaft, and that these terminations are much less strongly developed, the humerus of living lizard-like reptiles is very similar to that of their primitive relatives. The flexor process, at each end, is more prominent than the corresponding extensor, as originally. The plane of the distal extremity of the bone does not now lie quite at a right angle to that of the proximal end but at about 45 degrees because of some degree of inward rotation of the arm. The muscle plan, with minor adjustments, still conforms to the basic arrangement described above, except for the difference that the two divisions of the humerotriceps have invaded, on either side of the latissimus, the field of the axillary musculature, as shown in figure 2. Similarly the brachialis origin has moved proximally so that it comes to lie between the coracobrachial insertion and the origin of the humerotriceps lateralis.

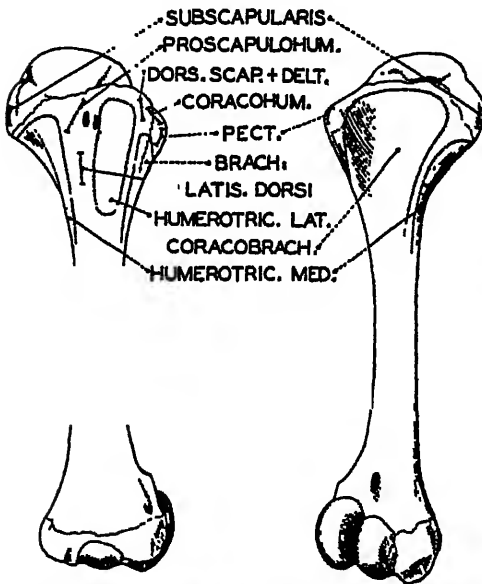


FIG. 2. RIGHT HUMERUS OF IGUANA, SHOWING AREAS OF MUSCLE ATTACHMENTS OF THE PROXIMAL END  
Dorsal view on left, ventral view on right

humeralis (later subscapularis)—was concerned with the retractor process posteriorly. It is likely that the first humeral association of *m. latissimus dorsi* was also with this process, but it probably shifted distally to a more favorable angle of leverage, appearing to have developed a process in the Rhachitomi at least. Later it shifted from one side of the shaft to the other as described in the discussion of this muscle.

At the distal end of the humerus the

#### NERVES

As in all other tetrapods the brachial plexus of living reptiles is built upon the three trunk plan. In Caudata the brachial axis is almost always through the fourth spinal nerve. Usually the third receives increment also from the second, which may be in the nature of a lag, and occasionally the sixth contributes to the fifth, being an added step in the posterior migration of the plexus. In the Salientia, with their high specializa-

tion and shortening of the spinal cord, there has probably been a secondary retreat cranialward, as well as concentration, of the plexus, so the axis is through the third nerve, with substantial contribution usually only from the fourth.

One may presume that in primitive reptiles also the plexus occupied a position more cranial than in mammals. In certain aberrant living forms, or if one prefer, those with more primitive nervous arrangement, such as *Pseudopus* and *Chamaeleo*, the axis of the plexus has migrated caudally only as far as the fifth spinal nerve (Fürbringer). At the other extreme is *Crocodylus*, with axis through the ninth nerve. Usually, however, this passes in modern reptiles through the seventh or eighth nerve, with a second and third trunk on either side of the central one. An additional root may contribute to either one of these peripheral trunks or to both (more often from above). Thus, there are usually at least four nerves supplying the plexus, occasionally but three as in the chelonian *Trionyx*, and at times five (some geckos and some iguanas). The plexus is supposed to arise from four roots in most lacertilians, but the discovery by me, only after intradural stimulation of the nerve roots, that some individuals, but not others, of *Iguana* receive a fine, very high, contribution also from n. 10, renders uncertain unverified assumptions that the plexus is limited to four roots. In *Iguana*, then, the brachial plexus arises from 4 or 5 spinal nerves, 6 to 9 or 10 inclusive, with axis through n. 8, the contribution from 6 being small, and that from 10, when it occurs, thread-like. In *Iguana* the brachial nerves are readily separable into a dorsal and a ventral group.

As already stated the nerve supply offers entirely dependable criteria for the identification of muscles, with an occasional

complication introduced by fasciculation. Thus if a muscle of one matrix comes to function with a second matrix, the nerve supply of that muscle will tend to align itself with the nerves of the second matrix. In other words, within certain limits the nerves of muscles which function together will tend to be grouped together, when no obstacle is encountered.

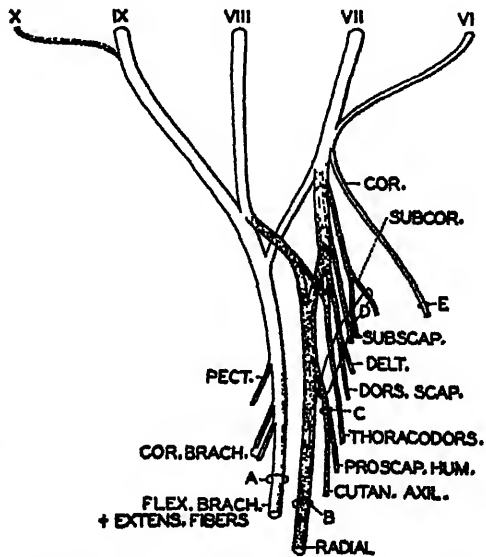


FIG. 3. RIGHT BRACHIAL PLEXUS OF IGUANA: SUPRAZONAL AND INTRAZONAL NERVES NOT INCLUDED

Dorsal division shaded, ventral division unshaded. A, passing between mm. coracobrachialis and humerotriceps medialis. B, passing between mm. coracoscapulotriceps and humerotriceps medialis. C, passing between mm. scapulotriceps and humerotriceps lateralis. D, nn. axillares communes. E, coracoid foramen.

In many cases nerve pathways are an invaluable aid to the interpretation of muscle homologies, providing that this criterion be used with care. If a slip separate from the surface of a parent muscle its nerve may pierce the muscle (i.e. coracobrachial head of the biceps in *Iguana*). But there is no certain evidence in myology that a muscle nerve ever migrates from one border of a muscle which it does not innervate to the opposite

border by successively piercing the muscle at different points. Where such appears to have been the case it is always some process such as a muscle origin retreating on one side of a nerve and then advancing upon the other side.

A brief discussion of the nerves supplying the shoulder muscles of *Iguana* is presented below. The determination of the derivation of individual branches has been tentatively established in part by the results of electrical stimulation.

*N. vago-accessorius*. Several fine branches, representing this component, diverge from the vagus and enter the sternocleidomastoideus, whence they are distributed to the remainder of the trapezius sheet. Entering this field are also nn. 3, 4, and 5.

*Nn. hypobranchiales*. These, to the hypobranchial musculature, are branches from n. hypoglossus, which receives contribution also from sp. nn. 1 and 2.

### Dorsal (extensor) division

#### Suprazonal group

*Rami musculares breves* from sp. nn. 4 to 9, supplying innervation of the mm. levator scapulae and serrati.

#### Shoulder group

*N. thoracodorsalis*. This is considered as separate from the axillary nerves only because it is so distinct in all tetrapods. It appears to be derived from nn. 7 and 8 (9?), and thus is located in the middle of the plexus much as in mammals, instead of upon the posterior border, from the last brachial root, as in Amphibia. This may indicate a shift in the relative position of its motor nucleus; but why this is the case one cannot say. The nerve supplies m. latissimus dorsi.

*Nn. axillares communes* constitute the remaining branches of the dorsal division supplying the shoulder musculature proper. The following branches may be

recognized: 1) *n. dorsalis scapulae* to the muscle of that name, and 2) *n. deltoideus* to the corresponding muscle. Both this and the last are twigs of a single axillary branch that is derived from n. 7, or 6 and 7, and which emerges from between mm. subscapularis and serratus superficialis. *N. deltoideus* crosses the deep belly of the m. dorsalis scapulae. 3) *N. proscapulo-humeralis* appears to be derived from n. 7, 8 (and 9?), and with an axillary cutaneous branch passes beneath the origin of the scapulotriceps to supply the muscle of the corresponding name. 4) *N. subscapularis*, single or double, appears to be derived from n. 7, or 6 and 7, and supplies m. subscapularis. 5) *N. subcoracoideus* to the muscle of this name, occurs either as a branch of n. subscapularis, or as an adjoining, independent branch of the plexus.

#### Brachio-antibrachial group

*N. radialis*. The nerve here termed radial follows, on the whole, the course usual in mammals. It passes between the heads of the scapulotriceps and humerotriceps medialis, in the brachium curving around between the two parts of the humerotriceps, which it innervates, and then piercing the ectepicondylar foramen. Additional dorsal fibers to the anti-brachium and manus, however, are incorporated in n. medianus, as described in a separate paper. Thus the long extensor nerve fibers of this appendage follow two pathways, as is frequently the case in Amphibia, but with a different arrangement.

### Ventral (flexor) division

#### Infrazonal group

These fine filaments come off the brachial nerves well dorsal to the actual plexus. They supply mm. costoscapularis and the two divisions of sternocoracoideus.

## Shoulder group

*N. pectoralis* is the dorsalmost branch of the common flexor trunk, as is frequent in Amphibia. It innervates *m. pectoralis*.

*N. coracoidens* is the most dorsal of the brachial nerves from the anterior cord of the plexus, as in Amphibia. It passes through the coracoid foramen before supplying the coracohumeral musculature and (secondarily) a small part of the coracobrachialis.

*Nn. coracobrachiales* appear usually to number two. They leave the common flexor nerve next below *n. pectoralis*, as in Amphibia. They disappear beneath the caudal border of *m. coracobrachialis superficialis* and innervate the coracobrachial matrix, including the proximal division of *m. biceps*.

## Brachio-antibrachial group

*N. flexor brachii*. This term might well be qualified, for the nerve also carries dorsal fibers to certain extensor muscles of the distal extremity. It passes between *mm. coracobrachialis* and *humero-triceps medialis*—not with *n. radialis*. In the brachium it gives off twigs to *m. brachialis* and the distal division of the biceps, before dividing into median and ulnar trunks. It is derived from the four posterior brachial nerves, but electrical stimulation indicates that fibers from *n. 10* innervate only the flexors of the wrist and manus.

## MUSCLES

The plan of musculature of living reptiles is separated from that of mammals by such an immense interval of time that there are naturally differences. That conditions in one group can be so satisfactorily interpreted in terms of the other is not only gratifying but quite astonishing. The shoulder musculature of *Iguana* may be described as follows:

## Branchiomic division

In this animal the accessory field is divisible into two contiguous portions.

*M. trapezius* has broad, aponeurotic origin from the dorsum. Insertion is peculiar in that the posterior portion is attached for several millimeters by fasciculi to the middle part of the anterior border of the suprascapula; while the more anterior part of the muscle inserts upon a ligamentous band attached at one end to the dorsal boundary of the insertion of the posterior portion of the muscle, and ventrally to the dorsal part of the clavicle, bridging the area between (fig. 4, C).

*M. sternocleidomastoideus* adjoins the last but is clearly separable. It is a much thicker division than the trapezius, originating by superficial aponeurosis from the posterior cranium, and by muscle fibers from the posterior border of the skull. Insertion is partly divisible, deeper fibers inserting upon the clavicle and more superficial ones upon the lateral process of the interclavicle.

In *Uromastix* conditions are essentially similar; this may be said of the insertions in *Sphenodon* but its trapezius is much less extensive; in *Cyclura* there is poor separation of the two divisions.

Innervation of the complex in lacertilians is by the spinal accessory nerve, and in addition several cervical nerves enter the muscle. In *Iguana* these are *nn. 3, 4, and 5* (4, 5, and 6 in *Sphenodon*).

It may prove tempting to consider the trapezius as representing a dorsal branchial constrictor and the sternocleidomastoid as a ventral constrictor. On the one hand there is no evidence in support of this thesis, and on the other Fürbringer (1900) has demonstrated that in recent lacertilians there are all stages encountered, from a simple undivided condition

of the accessory field to one in which the sternocleidomastoid is completely separable. Hence it appears that the latter is a derivative of a trapezius sheet.

In Amphibia spinal nerves to the trapezius have not been detected, but they occur in amniotes. In *Iguana* sensory fibers must follow this pathway. In some individuals, and in the alligator, no motor fibers could be found, by electrical stimulation, to reach the vago-accessory field via a spinal pathway, but in a particularly large individual motor fibers were found in nn. 3 and 4, but not in 5. Hence, in this respect reptiles doubtless are as variable as, if not more so than, are mammals.

#### Hypobranchial division

As explained in a previous part of the present study it is felt that no attempt should be made to homologize precisely the hypobranchial units of lower vertebrates with those of mammals. The same treatment will be adopted in the case of reptiles, admitting that such conservatism may not be justified, for the three divisions in *Iguana* show considerable similarity to the three divisions in mammals.

In *Iguana* the more dorsal division arises from the anterior border of the ventral half of the suprascapula and dorsal half of the clavicle, and inserts upon the lateral half of the hyoid. The middle division arises from the lateral process of the interclavicle and inserts upon the medial part of the hyoid and anterior part of the first (third) branchial cartilage, which in this form follows the midventral line. The third hypobranchial division arises from the anterior part of the interclavicle and inserts upon the dorsal surface of the anterior part of the first branchial cartilage. In *Sphenodon* there are but two divisions of this complex, one arising from

the border of the scapula and the other from both clavicle and interclavicle.

Innervation, reputedly by cr. n. XII, and sp. n. 1; not sought by me.

#### Dorsal (extensor) division

##### Suprazonal (or serratus) matrix

*M. levator scapulae* occurs in two divisions. Both arise apparently from the transverse process of the atlas only. The more superficial and larger pars dorsalis then diverges to insert upon the middle (not the anterior) third of the suprascapula, the posterior line of insertion being oblique and adjoining the origin of the dorsalis scapulae. The pars ventralis lies partially deep to the other division and inserts upon the ventral portion of the anterior border of the suprascapula.

*Iguana* is apparently representative of the lacertilian condition of the levator scapulae, while in *Sphenodon* the insertions of the two divisions are farther apart; these thus illustrate two of the stages in the separation of this muscle mass that culminates in certain mammals. In some reptiles (*Sphenodon*) origin is from the axis as well as atlas.

Innervation: Nn. 4, 5, and 6.

*Mm. serrati*. The complicated arrangement of the serrati in lizards has been exhaustively discussed several times and as they are of little importance to the present study a detailed description is not advisable. The slips occur in three groups: a) a posterior sheet, usually termed superficialis, extending ventro-caudally from the posterior border of the suprascapula to two ribs; b) a sheet two segments wide immediately beneath the suprascapula with fibers parallel to those of a); and c) a broader, deeper sheet covering four or five segments, with fibers inclined cranioventrally, and hence almost parallel to those of the levator



scapulae. Innervation is by the adjacent spinal nerves.

Undoubtedly the levator scapulae and serratus divisions have been differen-

the serratus. The superficial serratus depresses and retracts the suprascapula and is assisted by the more superficial sheet of the deep serratus. In mammals the

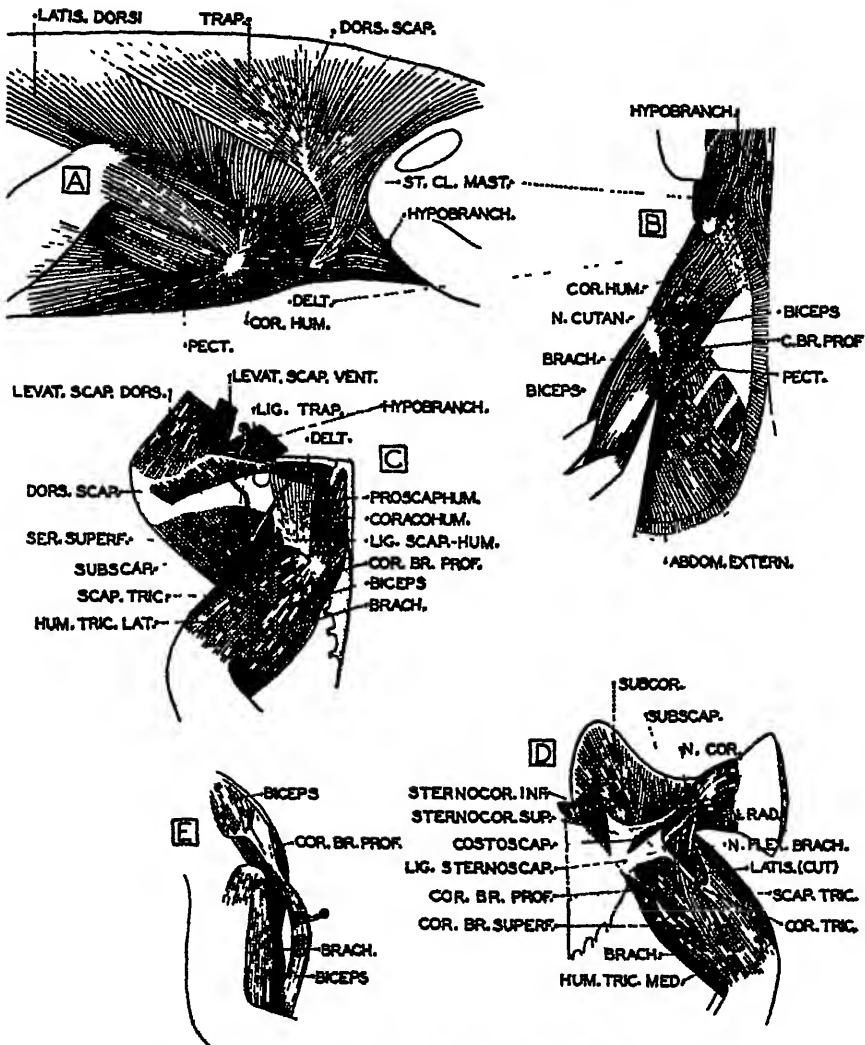


FIG. 4. MUSCULATURE OF THE RIGHT SHOULDER REGION OF IGUANA

A, superficial details in lateral view. B, ventral aspect, with pectoralis cut. C, lateral view of deeper details, vago-accessory field, part of hypobranchial musculature, and insertions of dorsalis scapulae, deltoideus, and pectoralis removed. D, medial view of shoulder. E, lateral view of brachial flexors; overlying muscles removed.

tiated from a single complex. The former advances and depresses the suprascapula and is assisted by the deepest sheet of

levator scapulae part remains distinct, and it is likely that the serratus divisions have experienced realignment so as to

operate on a more mobile scapula in a single sheet. Romer (1922) is of the opinion, however, that the reptilian serratus superficialis is not represented in mammals.

A rhomboid division has not been developed in modern reptiles except by the Crocodilia.

#### *Shoulder group*

##### Thoracodorsal (latissimus) matrix

*M. latissimus dorsi* has broad origin in *Iguana*, extending anteriorly so as to cover a part of the dorsalis scapulae. It converges to a tendinous insertion upon the more dorsal part of the protractor (flexor) process of the humeral head. Conditions are similar in *Sphenodon*. Innervation: N. thoracodorsalis (from nn. 7, 8, and 9?).

The interesting point in regard to the latissimus is the manner in which its insertion has migrated. In *Necturus* its pull is in the same plane as the triceps group. Hence it is an extensor of the upper arm, without rotational action. In *Rana* the insertion has shifted to one extreme, over the lateral surface of the humerus to the flexor tuberosity. Hence the muscle not only has a longer pull, but is a lateral rotator as well as a retractor of the arm. This is doubtless correlated with the extreme akimbo position in which the anuran arm is held. In *Iguana* the latissimus insertion has shifted toward the opposite extreme, having migrated medially to an association with the brachial flexors; so that in lacertilians it is not only a retractor but a powerful inward rotator of the arm. This action helps in the fact that in this group flexion of the arm is not straight back, but is accompanied by abduction of the elbow. This shift in the attachment of the latissimus insertion is further explained in connection with m. triceps.

It may here be mentioned that derivation of the mammalian m. teres major is probably from the latissimus sheet, as believed by Romer (1922).

##### Axillary matrix

This includes those muscles of the dorsal division which arise from the girdle and insert upon the humerus.

*M. dorsalis scapulae* has origin along an oblique line, adjoining that of m. levator scapulae, which extends from a point near the dorsocaudal part of the suprascapula toward the clavicle. Here origin is both from the dorsal part of the clavicle and from the dorsal margin of the first fenestration of the girdle. A part of the origin is covered by the latissimus (beneath trapezius in fig. 4 A). At insertion the fibers fuse with those of the deltoid and attachment is narrowly upon the lateral part of the protractor process of the humeral head.

Conditions are essentially the same in *Cyclura* and *Sphenodon* except that in the latter origin is more dorsal, rather than oblique. This detail in *Necturus* is also much the same.

Innervation: A branch of the axillary nerve which enters the muscle along its posterior margin.

It seems evident that in basic forms, such as stegocephalians, this was *the* girdle muscle of the cleithrum, just as the deltoid is *the* girdle muscle of the clavicle, and that the two were not only contiguous, but that to all intents the sheet comprised a single muscle. As the cleithrum disappeared the dorsalis scapulae component settled upon the suprascapula and became separated to various degrees from the deltoid. There is no reason for presuming, as do Romer and others, that the two divisions ever fused again to constitute the mammalian deltoid. On the contrary there is every

reason for believing, and none for doubting, that the dorsalis scapulae later became the *teres minor*.

*M. deltoideus* (proscapulohumeralis part) is not attached to the cartilaginous girdle at any point but has origin from the inner margin of the ventral two-thirds of the clavicle and inner surface of the anterior interclavicle. Its fibers fuse at insertion with those of *m. dorsalis scapulae*, and attachment is upon the lateral part of the protractor process of the humeral head. In *Sphenodon* conditions are similar except that origin is purported to be from the lateral aspect of the clavicle (Miner).

Innervation: A branch of the axillary nerve, from nn. 6 and 7, from which also diverges the twig to the dorsalis scapulae. Beneath the latter muscle it passes to the cranial part of the deltoid.

There appears to be but little doubt that *m. deltoideus* was basically clavicular in origin. Where the clavicle disappeared the muscle settled upon the cranioventral part of the scapula, becoming a scapulohumeralis longus, as in *Caudata*. A tendency which it exhibits throughout phylogeny is a dorsal migration of its origin. In claviculate Salientia dissociation of the deltoid origin from the clavicle is practically complete, origin being from the girdle dorsal to that bone. In laceratilians it is still entirely from that bone, and hence has nothing to do with the cartilaginous girdle.

*M. proscapulohumeralis* (procoracohumeralis brevis, scapulohumeralis anterior). At origin, which is from the lateral surface of the girdle around the anterior margin of the second fenestration, this muscle immediately adjoins *m. coracohumeralis* and is in the same layer. Toward insertion, however, the latter muscle passes over the ligamentum scapulohumeral while *m. proscapulohumeralis* passes beneath the ligament to insert

upon the humerus between the lateral and medial heads of the humerotriceps. Conditions appear to be the same in other lizards considered. Innervation: By a branch of n. axillaris, passing deep to the origin of the scapulotriceps.

The *mm. deltoideus* and proscapulohumeralis are separated by the tough fascial extension of the ligamentum scapulohumeral, and if such separation were fundamental it would constitute evidence for considering the two muscles to have had separate derivation. The ligament has probably been secondarily developed, however, and it is believed that the proscapulohumeralis of *Iguana* is homologous to the shorter division of the same name in *Necturus*, and that it represents a deeper division of the original dorsalis scapulae—*deltoideus* layer.

*M. subscapularis* (scapulohumeralis brevis or posterior) arises from the base of the medial side of the suprascapula and adjoining part of the scapula, and from the caudal border of the latter, barely encroaching upon the lateral surface. The fibers converge to tendinous insertion upon the retractor process of the humerus. The function is inward rotation with slight retraction of the arm. Innervation: By an axillary branch that pierces the medial surface of the muscle.

It is considered that this muscle is homologous to the scapulohumeralis brevis (termed subscapularis in *Megalobatrachus* by Miner) of amphibians, which in reptiles has invaded and spread over the medial surface of the scapula. In *Iguana* and *Cyclura* it is indivisible, but in *Sphenodon* a scapulohumeral slip is distinct from the remainder of the subscapular portion. This separation is probably secondary.

*M. subcoracoides* adjoins the subscapularis but is separated therefrom by the scapular attachment of the sternoscapular

ligament and by n. coracoideus. It is largely multipennate in form and arises from the entire medial surface of the coracoid, passes deep (lateral) to the sternoscapular ligament, and inserts upon the capsule of the shoulder joint continuous with the tendon of the subscapularis. It must act as a retractor of the arm. Innervation is either by a twig from one of the branches to m. subscapularis, or by a separate branch leaving the plexus close to n. subscapularis. This frequently follows n. coracoideus for a short distance.

The most logical explanation of the derivation of this muscle is that initiating fibers first diverged from the subscapularis near insertion, and then spread over the medial surface of the coracoid between the bone and the sternoscapular fascia (ligament). The innervation lends strong support to this thesis. Certainly it is a muscle of the dorsal division and there is no other logical source from which it could have come.

Gregory and Camp consider that this slip is represented in mammals by m. coracobrachialis brevis, an entirely unjustifiable conclusion. I subscribe to the opinions of Romer and Miner that the muscle must have been undeveloped, or at least purely vestigial, in early reptiles and mammal-like reptiles, and unrepresented in mammals, because the conformation of the girdle in the first renders it almost impossible that such a muscle could have been effective, as would certainly be the case as soon as the humerus had begun to be held in the typical mammalian position. It therefore follows that the muscle was differentiated only in forms in which the humerus was held in an essentially retarded position and largely parallel with the ground.

*Ligamentum axillaris.* This is a complex structure an adequate description of which I have not encountered in the literature,

but which may be of much importance. It may be considered to consist of two connected portions, termed scapulohumeral and sternoscapular ligaments. The scapulohumeral ligament is largely triangular in form, the dorsal angle being attached to a slightly defined process on the lateral scapular margin just above the glenoid, the ventral angle to the lateroventral process of the humeral head, while the posterior angle of the ligament provides origin for the scapulotriceps fibers. The anterior border of this ligament continues cranially as a tough, aponeurotic fascia, between mm. deltoideus and proscapulohumeralis. The part that forms the tendon of the scapulotriceps extends in a loop distally around the insertion of the latissimus and then continues proximally as the tendon of the coracotriceps, passing to the medial aspect of the girdle. Proximal to the axillary border of the coracoid this tendon spreads out to form the sheet termed sternoscapular ligament. It has a three-point anchorage; 1) broadly along the coracoid border of the sternum and thence continuously to 2) the medial border of the coracoid, and narrowly to 3) the medial surface of the scapula. Upon the medio-dorsal surface insert the fibers of the costoscapularis, ventral to it is situated m. subcoracoideus, and covering a part of its dorsal surface is m. sternocoracoideus. In addition, from the medial border of the proximal part of the coracotriceps tendon diverges a tough sheet of fascia which is attached to the humerus deep to the insertion of the coracobrachialis. Thus in *Iguana* the scapulo- and coracotriceps arise from a continuous, tendinous sling or loop, suspended laterally between scapula and humerus, and medially between sternum, coracoid, and scapula. This is a very striking and strongly developed arrangement which may shed

considerable light upon the derivation of triceps divisions.

In *Cyclura* this arrangement is less strongly defined but on the whole is similar, except that the scapulotriceps arises more from the scapula and not so definitely from the stout scapulohumeral ligament. In *Sphenodon* m. scapulotriceps appears to be intermediate between conditions in *Iguana* and *Cyclura*, but descriptions of *Sphenodon* do not stress nor clearly indicate continuity between the tendons of the scapulo- and coracotriceps.

Ligaments are derived from connective tissue and not from bone; hence the sternoscapular ligament hardly is a remnant of the primitive supraglenoid buttress, as argued by Miner, but very possibly of the fascia that was concerned therewith. If derivation of these ligamentous sheets had been purely from capsular ligaments they would occur deep to all the muscles; but they are situated superficial to certain muscles; hence it seems clear that they have developed from fascia. This is further discussed in relation to the triceps.

#### *Brachio-antibrachial group*

It is convenient to recognize by name four divisions of the anconeus or "triceps" complex in *Iguana* as follows:

*Mm. scapulotriceps et coracotriceps.* These are virtually inseparable but it is convenient to differentiate the fibers concerned with the two sides of the girdle. Those considered scapulotriceps arise from the scapulohumeral ligament and from the continuation thereof which loops around the insertion of the latissimus. From the medial part of this tendinous loop arise the fibers of the coracotriceps, the ligament therefrom continuing proximally as a round tendon with attachment to the sternoscapular ligament (fig. 4 C). Common insertion is upon the olecranon.

*M. humerotriceps lateralis*, between nn. scapulotriceps and brachialis, arises from the caudolateral part of the humeral head and adjacent part of the shaft. Insertion is upon the olecranon.

*M. humerotriceps medialis*, located between the flexor brachii and extensor brachii, takes origin from the medial head of the humerus just caudal to the insertion of the subscapularis, and from practically the entire length of the shaft of this bone. Insertion is upon the olecranon.

Innervation: Branches of the common extensor nerve or n. radialis.

The same difficulty in interpreting the phylogeny of the brachial flexors is encountered in the extensors of this segment. Because of conditions in *Necturus* it is considered possible that its dorsitriceps (representing a scapulotriceps) may have been derived from the latissimus, aberrant slips having extended down the arm via a fascial route. Even if this was actually the case, however, mergence with the rest of the triceps is so far advanced that one can be certain of nothing: and the situation is, of course, still more obscured in reptiles. With this possible exception, however, I am unable to escape the belief that the triceps has been derived from a brachio-antibrachial matrix, originally having nothing to do with the shoulder. Whatever the primitive origin of the "scapulotriceps" the diversification of its subsequent development indicates that it was not originally connected with the girdle, but that it has experienced during its phylogeny an essentially constant stimulus for reaching the scapula. Or let us express it that there has been a stimulus for some part of the triceps to reach the scapula. In *Rana* origin shifted so as to pass medial to both the latissimus and dorsalis scapulae and eventually reach the scapula; and the fact that it bridges

n. pectoralis indicates that its route was fascial rather than via bone and joint capsule. Furthermore, the fact that in *Rana* it did not encounter the obstacle of the tendon of the latissimus renders it likely that in function, and probably in fact, this head in the frog represents both scapular and coracoid triceps. In *Iguana* it has attained the same functional goal, but by another pathway, which carries it lateral to the latissimus tendon. In this case also the pathway has probably not involved a bony attachment, but migration along a fascial plane, which carried it superficial to the insertion of m. proscapulohumeralis with the arrangement already described. It is only thus that differences in the muscle can be explained.

There is considerable question whether the coracotriceps of *Necturus* is homologous to the corresponding slip in reptiles. Its origin, from flexorward of the brachial nerves, introduces some uncertainty, and the fact that Miner found the proximal part innervated by a twig of n. coracobrachialis in *Megalobatrachus*, which is not the case in *Necturus*, suggests a dual origin. Romer considered that there was no coracotriceps in primitive reptiles, and the division is absent in mammals. In *Rana* an indivisible scapulotriceps subserves the function of both, but in lizards the latissimus tendon intervenes as an obstacle, and this has been overcome by the development of two origins, from scapula and coracoid respectively, for an otherwise indivisible, long triceps. It appears that even in these the coracotriceps part is in course of reduction. Further argument along this course suggests that one would not expect to encounter a coracotriceps separated from a scapulotriceps unless the latissimus tendon is so situated as to require straddling by the long triceps division.

The humerotriceps divisions have shifted around to some extent, and there are indications that there have been recession and advance of their origins. Thus the lateralis in *Rana* has advanced in a proximal direction lateral to the tendon of the latissimus, while in *Iguana* this advance has been medial to the tendon. In *Necturus* the proximal advance of the medial head has been posterior to both flexor and extensor nerves of the brachium, while in *Rana* this head separates the respective nerves, as is also the case in *Iguana*. It is probable that a fairly safe criterion for differentiation of the two heads of the humerotriceps is the course of the radial nerve, which passes between them.

In *Sphenodon* there is an additional brachial extensor — humeroradialis — which is absent in other lizards but which is purported to have a partial homologue in Crocodilia (Fürbringer). It arises from a distal continuation of the ventral part of the scapulohumeral ligament, and inserts partly upon the supinator longus of the forearm. As it is proximally innervated by a twig of the deltoid branch and distally by n. radialis lateralis, it is probably compounded of deltoid and supinator elements (Miner).

#### Ventral (flexor) division

##### Infrazonal matrix

There is no certainty that this group should not be accorded a separate division, like the hypobranchial matrix, but it can be included provisionally with the ventral division of the girdle musculature. In *Iguana* it is differentiated into three slips as follows:

*M. costoscapularis* (costosternocoracoid) is the most lateral, arising narrowly from the first sternocostal and inserting upon the dorsal surface of the more lateral part of the sternoscapular ligament.

*M. sternocoracoideus superior* (sternocor. profundus) is the broadest of the group, arising from the dorsal surface of most of the sternum, and inserting by a broad, thin tendon upon the caudomedial part of the coracoid, on a line parallel with the fibers of the subcoracoideus, muscle fibers of the latter passing upon both sides of the line of insertion.

*M. sternocoracoideus inferior* (sternocor. superficialis) is much smaller and entirely hidden by the superior division. Origin is from the medial part of the anterior border of the sternum, between the sternoscapular ligament ventrally and the fascia or ligament of the sternocoracoid articulation. It inserts with the superior division.

Innervation: By high, slender filaments from all three brachial trunks, most of that from the first supplying the costoscapularis.

The first two of these muscles are rather uniform in lizard-like reptiles, while the group appears to be represented in all living members of the order (except those without girdles). The third is more variable. In *Sphenodon* origin is more extensive, from not only the entire cranial border of the sternum but also from the first sternocostal. Occasionally it appears to be absent (*Uromastix*).

Miner looks upon this group as a remnant of the sternohyoid musculature, and hence as an anterior representative of the rectus abdominis. This I consider a more precise commitment than the evidence warrants. It appears much better to regard the group merely as ventral slips of the trunk musculature originally passing from the body to the membranous girdle, entirely comparable to the more dorsal *serratus matrix*.

This group is absent in Amphibia but there is no reason for doubting that it was present in ancient reptiles and in the

mammalian ancestry. Its mammalian representative is rather uniformly considered to be *m. subclavius*, to which hypothesis there appears to be no objection; but no attempt should be made to homologize the latter muscle with any one of the slips occurring in living reptiles.

### *Shoulder group*

#### Pectoral matrix

*M. pectoralis* arises from the full length of the interclavicle and from the border of the diverging "xiphisternum," as well as for some distance from the last complete rib. The fibers converge to a narrow insertion upon the ventral process of the proximal humerus. The muscle is partly divisible into a mesocleido-xiphisternal part, and a part originating from the rib. The former is paler colored and the latter more reddish, this difference suggesting some corresponding difference in action. Innervation: *N. pectoralis*, by way of the axilla, from the posterior part of the plexus.

In *Sphenodon* the posterior part of this muscle has extended beneath the border of the superficial abdominal muscle, rather than superficial to it as seems usual in lacertilians. In *Iguana* it also extends more dorsally than in *Sphenodon*.

If one consider that the pectoralis of *Necturus* illustrates an intermediate condition, in which this sheet covers practically none of the coracohumeral (supracoracoid) musculature, then modern reptiles represent one direction of pectoral development, with the muscle covering the coracohumeral layer entirely and with extreme anterior extension, while mammals illustrate an opposite trend, in which the coracohumeral layer over-rides the pectoralis, in some forms (man) covering all of the latter muscle.

Mention should here be made of the

mesocleidosternal ligament (fig. 4 B), which is broad and tough, passing from the lateral process of the interclavicle to the anterior border of the sternum, and located just deep to *m. pectoralis*. Fürbringer (1900) stated that in lacertilians the episternal part of the "sternocleidomastoid" inserts upon this as well as the lateral process, and his figures of *Gekko*, *Zonosaurus*, and *Lygosoma* indicate not only that he considered the relationship of the muscle and ligament very close, but that the latter extends lateral to the process. In *Iguana* this feature did not obtain, but the sternocleidomastoid fibers have nothing to do with the ligament except that a few of them spread over the interclavicular attachment. There is no necessity for considering such ligaments as the remnants of muscles, and it does not seem wise to look upon this one as indicating a former extension of the rectus abdominis. It is really a broadened fascia or ligamentous connection between interclavicle and sternum, and no attempt should be made to make anything more of it.

#### Anterior coracoid matrix

*M. coracobromalis* (supracoracoideus), although not extensive, is a very stout muscle, especially in large individuals. It arises from the anterior margin of the two inferior (third and fourth) fenestrations of the girdle, converging, mostly under cover of *mm. deltoideus* and *pectoralis*, to an insertion just proximal to that of the latter muscle. Innervation: N. coracoideus, diverging from the anterior part of the plexus and piercing the coracoid foramen.

The anterior coracoid musculature is secondarily simplified in lacertilians as compared with *Necturus*, and especially *Rana*. Presumably it is also more simple than it was in Lower Permian reptiles.

Thus, living reptiles show no initiation of the changes which this matrix experienced in the development of the suprascapular musculature and the *pectoralis major* of mammals. Dicynodonts and theriodonts, however, and also some of the still older reptiles in lesser degree, indicate by the reduction of the anterior part of the coracoid that a part of the origin of the coracobromal musculature probably had settled down upon the sternum, thus initiating a *pectoralis major* component. Similarly, in these forms the conformation of the acromion shows very plainly that a part of this matrix had migrated dorsally, anterior to the acromion, and thus deep to the insertion of the trapezius. This part evidently did not encroach upon the lateral surface of the scapular blade but at first must have been largely confined to the anterior border. Thence fibers could extend posterior to the acromion around its ventral termination, to become an *infraspinatus*, and medially, to become the anterior part of the *subscapularis*. That some of the anterior coracoid musculature still originated from the coracoid in these reptiles, however, is indicated by the survival of the anterior division of the ventral part of the girdle.

#### Posterior coracoid matrix

Four divisions of the coracobrachial group are clearly separable in *Iguana*, and because of their possible importance in later discussion they will be described at some length.

*M. coracobrachialis superficialis* (*coracobrachialis longus*). This is divisible into two parts, one (a) with tendinous origin, and the other (b) with fleshy origin. The former arises by a long tendon from the extreme posterior termination of the metacoracoid region of the girdle. Insertion is partly upon the medial epicondyle



of the humerus and partly upon the stout flexor-extensor intermuscular septum of the brachium. Part b) is located superficially between the tendons of part a) and coracotriceps. It has fleshy origin from the medial aspect of the sternal border of the posterior coracoid, passes, like part a), superficial (medial) to n. flexor brachii, and also inserts upon the flexor-extensor intermuscular septum of the brachium. Innervation: Twigs of n. coracobrachialis, and also by another filament diverging from the flexor nerve somewhat below, both passing deep to part b) of the muscle.

This arrangement in *Iguana* appears to be different from the usual condition in lizard-like reptiles, as typified by *Cyclura*, *Uromastix*, and *Sphenodon*, in which the muscle is not readily separable into two parts, and without a definitely tendinous origin. Because of this one may infer that the tendinous head is accessory to the other, possibly having reached its present form by adopting a fascial pathway or appropriating some such structure as the coracoradial tendon of *Megalobatrachus*. Similarity of innervation and of association with the intermuscular septum, as well as situation with respect to the flexor nerve, indicate the unquestionably close relationship of the two divisions.

*M. coracobrachialis profundus* (coracobrachialis brevis) likewise occurs in two parts, both of which lie deep (lateral) to n. flexor brachii. The more extensive part a) is covered mostly by the biceps, having origin from the lateral surface of the part of the girdle bounded by the posterior process of the coracoid, the glenoid prominence, and the posterior border of the inferior fenestration. Fibers pass, deep to the biceps tendon, to insert upon the proximal half of the medial aspect of the humerus. Part b) is a small

slip located between part a) and m. coracobrachialis longus, originating from the tip and adjoining posterior border of the posterior coracoid process, and inserting with the other division, but medial to it. Innervation of part b) is solely by n. coracobrachialis, which passes deep to it. Part a) is innervated chiefly from this source, via its deep belly, but also it indubitably receives a fine filament of n. coracoideus, which enters the lateral border of the muscle near its origin.

Conformation and innervation are the same in *Cyclura*, but in other lizards reported in the literature the muscle appears to be single, and partial innervation by n. coracoideus appears never to have been detected. To my mind this double innervation is interesting as indicating that a part of the coracohumeral (supracoracoid) musculature, probably representing the coracohumeral minor of *Necturus*, has secondarily become associated with the coracobrachialis profundus, but it is evidently either of transitory significance or else is a development unique in certain lizards, for it appears not to be found in other animals.

#### *Brachio-antibrachial group*

The biceps of *Iguana* is a product of both this and the posterior coracoid matrix, but chiefly of the former.

*M. biceps brachii* is single but occurs as a proximal belly and a distal belly, the two separated by tendon. The former is short, thin, and fan-shaped, arising from the anterior border of the inferior fenestration of the girdle, deep to m. coracohumeralis. Fibers converge to the lateral side of a broad tendon which, deep to the muscle, arises partly from the posterior border of the inferior fenestration and partly from the medial border of the girdle. The tendon passes partly beneath the head of

the humerus and from it arise the muscle fibers of the distal part of the biceps. There is partial fusion distally with the brachialis, but nevertheless insertion of the biceps is essentially upon the ulna. Innervation of the proximal belly is by a branch of n. coracobrachialis, which enters the deep surface after piercing m. coracobrachialis profundus. The distal part of the muscle is supplied by a branch, in close association with that to the brachialis, of n. flexor brachii.

This is the arrangement of the biceps typical of lizards, varying from the condition in which the proximal belly inserts upon the whole width of the tendon (*Gecko*, as well as *Sphenodon*), to that in which the fibers have finally disappeared and the tendon becomes narrow (*Chamaeleo*), as figured by Fürbringer (1900). Conditions in the vertebrates indicate a constant effort to evolve a satisfactory "biceps" out of any material that was ready at hand (*Megalobatrachus*, *Necturus*, *Rana*). In *Necturus* it is not unlikely that the coracobrachial complex was so employed to manufacture m. gleno-anti-brachialis. It seems apparent, however, that the lacertilians have either followed a different plan, or less likely that in them a coracobrachial derivation of the distal biceps has been secondarily obscured. At least in their case conditions suggest that the lower division of the biceps became initiated by the divergence of a distal part of the brachialis onto a fascia or intermuscular septum, along which the fibers extended proximally. That this was so is indicated by the association of the nerve to the distal biceps with that to the brachialis. The separate nerve supply to the proximal part of the biceps very clearly shows that that, at least, was derived from a part of m. coracobrachialis which secondarily settled upon the tendon of the biceps. That this

proximal part is unrepresented in mammals is highly likely.

*M. brachialis* originates laterally from the head of the humerus and most of its shaft, between mm. biceps and humero-triceps lateralis. Near insertion there is partial fusion with the biceps, but artificial separation demonstrates that insertion of the brachialis is upon both radius and ulna. Innervation: A branch of n. flexor brachii.

This muscle is considered to be fundamental, constituting a matrix of its own, from which has been derived the part of the biceps brachii which is represented in mammals.

#### DISCUSSION OF NERVE-MUSCLE ACTION

In the present study the stimulating apparatus used was that described in Part III. Action through motor fibers, by applying current to intact nerves or to the peripheral stumps of nerves that had been cut, was uniformly obtained on animals under ether anesthesia at a threshold not exceeding one quarter volt. Muscular response via particular sensory pathways was secured by applying stronger current, of one half to one volt, to the central stumps of certain nerves that had been transected. It is as yet unknown just what type of sensory fibers carry these electrically excitable impulses—whether they have heretofore been grouped with proprioceptive or some other sort of afferent fibers. Hence, for the present, they will be designated merely by the innocuous term of x-afferent fibers, the "x" indicating the unknown quantity. It is probable that in normal muscle action these fibers constitute the afferent parts of reflex arcs which are brought into play by stimuli supplied by the stretching of muscles, movement of joints, and similar phenomena. In the tests conducted

five specimens of *Iguana* were variously employed in three sets of experiments.

*Experiment on the innervation of the accessory field.* Five sides of three specimens. The accessory field in *Iguana* is innervated by a group of several fine branches of the vagus, representing a spinal accessory component, and by nn. 3, 4, and 5. The accessory branches enter the extreme anterior border of the muscle sheet, and the spinal nerves farther back. The three spinal nerves were cut. Stimulation of their respective *central* stumps at currents from  $\frac{1}{2}$  to 1 volt resulted as follows: Through stump of n. 3, no action of the accessory field, but only a slight tremor of the adjacent trunk musculature; through n. 4, contraction of the sternocleidomastoid only; and through 5, contraction of the trapezius only, particularly the posterior part (not determined in one animal). Stimulation of the *peripheral* stumps was without result in one individual. In a second there was no action through nn. 4 and 5, but n. 3 was damaged and not tried. In a third, particularly large specimen there was strong action of the sternocleidomastoid through n. 3, on both sides; of the trapezius through n. 4 on one side but not on the other; and no determinable action through n. 5.

This experiment indicates that in some cases all the motor fibers to the accessory field of musculature are carried only by N. XI (or its equivalent), while in others a portion of these fibers follow a spinal pathway, those to the sternocleidomastoid being situated more cranially than the ones to the trapezius; that n. 3 carries x-afferent fibers discharging into motoneurons supplying the trunk musculature only; that n. 4 carries similar fibers concerned with the sternocleidomastoid, and n. 5 with the trapezius. A larger series would doubtless show variation from this pattern.

It thus seems that some of the fibers which in anamniotes follow a vago-accessory pathway have, in amniotes, adopted a shorter route. This question is more fully discussed in collaboration with W. L. Straus, Jr. in a paper now in press.

*Experiment on brachial plexus: Peripheral approach.* The trapezius and serrati were transected and the suprascapula abducted to expose the brachial trunks where these emerge from beneath the dorsal musculature.

*Series A.* Three sides of two specimens. The three brachial trunks were cut and muscular contraction obtained by stimulating the *peripheral* stumps at low voltage (ca. one-eighth volt). Through trunk 1 there was strong flexion of the anti-brachium and moderate flexion of the digits. The brachium was held at a right angle to the body (thus protracted) and two actions were then involved, following separate stimulation of the two borders of the one trunk (evidently because sp. nn. 6 and 7 both contribute to it): a) adduction, and b) slight abduction of the brachium. Through trunk 2 there was rigid extension of the entire limb in a ventral direction. Through trunk 3 there was similar extension of the arm but in a more caudal and lateral position; digits either lax or slightly flexed. In one instance the above action of trunks 2 and 3 showed some reversal. Results otherwise were quite uniform. In another instance the action through trunk 1 could not be repeated subsequent to the application of one-and-a-half volts. Stimulation at one volt of the *central* stumps of the brachial trunks was followed by lateral wriggling of the body.

This experiment indicates that there is the same plan of motor control of the limb as occurs in *Necturus*. The first trunk carries impulses for flexing and protracting the limb beneath the body, the second

initiates extension, and the third completes it, with some intervariation in the action through the two posterior trunks. It should be realized that from this approach the responses are somewhat mixed, for the first brachial trunk carries fibers from sp. nn. 6 and 7, and the third, fibers from 9 and sometimes 10. In *Necturus* there was secured through the third trunk, at a higher threshold, an initiation of recovery toward the flexed position of the limb. This was not observed in *Iguana* during this experiment. At no time was the elbow advanced farther cranially than the level of the glenoid, further protraction doubtless being secured through action of the accessory and hypobranchial fields. The experiment also indicates that action of the limb muscles stimulates, through x-afferent fibers, contraction of the adjacent trunk musculature.

*Series B.* Both sides of one specimen. On the right side brachial trunks 1 and 3 were sectioned and the central stumps were stimulated. At one-quarter volt there was a tremor toward supination of the wrist. At one-half volt both roots had the same action, violently extending the limb straight back against the body. The same voltage applied to the intact trunk 2 had an identical result. On the left side trunk 2 was cut, leaving trunks 1 and 3 intact. The central root of trunk 2 was stimulated at one-tenth volt without result. As one-half volt there was first contraction of the adjacent trunk musculature, followed after 1 second (circa) by wriggling of the body and movement of all four limbs.

This experiment indicates that x-afferent fibers are carried by trunks 1 and 3; that at least some of these connect centrally with motoneurons whose axons emerge via trunk 2; and that none of the x-afferent fibers possibly carried by trunk

2 are concerned with motor axons emerging by trunks 1 and 3.

*Experiment on brachial plexus: Intradural approach.* The spinal cord of a lightly etherized *Iguana* was exposed by laminectomy to include what I thought at the time were segments 6 to 10. Autopsy, however, proved that access was thus given to the roots of nn. 7 to 11 inclusive. The dura was slit and reflected. Stimulation at about one-half volt of the intradural part of the dorsal roots of these nerves resulted as follows: Through 7, flexion of forearm with slight protraction of arm; through 8, retraction of extended limb, with action more contralateral than ipsilateral; through 9, retraction with abduction of extended limb; through 10, flexion of wrist only, with moderately extended limb; and through 11, no movement ipsilaterally but indefinite, though quite strong, action by the contralateral member. In all cases there was some vague contralateral, and at times, diagonal limb movement.

The dorsal roots were then cut and the ventral roots stimulated at one-eighth volt, with the following results: Through 7, adduction with slight retraction of brachium, and flexion of antibrachium; through 8, strong retraction of extended arm; through 9, strong retraction, with some abduction, of extended arm; through 10, some retraction of extended arm with flexion of the wrist; and through 11, with current increasing to 1 volt, no action of arm, but slight contraction of trunk. The experiment upon the opposite side was incomplete, because of damage to one of the nerves, but the partial results were in conformity with those obtained contralaterally.

The cord of a second, large animal was exposed between nn. 4 to 8 inclusive. Stimulation of the dorsal roots of nn. 4 and 5 resulted in ipsilateral contraction of

m. levator scapulae; of n. 6, protraction of brachium and flexion of antibrachium on both sides; of n. 7, largely as last, but ipsilaterally only and with more retraction; and of n. 8, ipsilateral retraction of arm, with retraction of both hind legs and curvature of tail to that side. Stimulation of the ventral roots after cutting the dorsal roots resulted very similarly, except that through n. 8 there was more extension of the forearm.

This experiment suggests that the dorsal roots of all the brachial nerves carry x-afferent fibers, the action resulting from their stimulation matching to a large degree the effect of stimulation of the

corresponding ventral roots, with the exception that those of n. 6 are almost equally contralateral in action, and those of n. 9 almost exclusively so. The more peripheral experiment also tends to verify the latter statement. In addition, at least the first of the thoracic nerves posterior to those contributing to the plexus carries x-afferent fibers to connect with motor-neurons of the contralateral member. Stimulation of the ventral or motor roots obtained results essentially similar to those performed more peripherally, as already described, except that they suggest that n. 10 carries axons only to the flexor musculature of the distal part of the limb.

#### LIST OF LITERATURE

(Exclusive of most titles listed in Parts I, II, and III)

- BOGOYUSKY, S. 1914. Brustbein- und Schultergürtelentwicklung bei einigen Lacertilien. *Zeitsch. wiss. Zool.*, Bd. 110, S. 621-666.
- BROOM, R. 1912. The morphology of the coracoid. *Anat. Anz.*, Bd. 41, S. 625-631.
- FÜRBRINGER, MAX. 1875. Zur vergleichenden Anatomie der Schultermuskeln. Teil III. *Morph. Jahrb.*, Bd. 1, S. 636-816.
- . 1900. Zur vergleichenden Anatomie der Brustschulterapparates und der Schultermuskeln. Teil IV. *Jena. Zeitsch. Med.*, Bd. 34, S. 215-718.
- GEILDEREN, CHER. VAN. 1913. On the development of the shoulder-girdle and episternum in reptiles. *Konink. Akad. Wetens. Amsterdam*, Bd. 26, S. 15-31.
- GREGORY, W. K., AND C. L. CAMP. 1918. Studies in comparative myology and osteology: No. III. *Bull. Amer. Mus. Nat. Hist.*, vol. 38, pp. 447-563.
- GÜNTHER, A. 1867. Contributions to the anatomy of *Hatteria* (*Rhynchocephalus*) Owen. *Philos. Trans. Royal Soc.*, vol. 157, pp. 595-629.
- HANNON, F. B. 1920. The problem of the coracoid. *Anat. Rec.*, vol. 19, pp. 327-341.
- HEERWIG, O. 1906. Handbuch der vergleichenden und experimentellen Entwickelungslehre der Wirbeltiere. *Jena*. Bd. 3, T. 2, S. 167-270.
- HOFFMANN, C. K. 1879. Beiträge zur vergleichenden Anatomie der Wirbeltiere. XII. Zur Morphologie des Schultergürtels und des Brustbeins bei Reptilien, Vögeln, Säugetieren und dem Menschen. *Niederl. Arch. Zool.*, Bd. 5, S. 31-106.
- HOWES, G. B. 1887. The morphology of the mammalian coracoid. *Journ. Anat. Physiol.*, vol. 21, pp. 190-198.
- MINER, R. W. 1915. The pectoral limb of *Eryops* and other primitive tetrapods. *Bull. Amer. Mus. Nat. Hist.*, vol. 51, pp. 145-312.
- NEWMAN, A. K. 1877. Notes on the physiology and anatomy of the Tuatara (*Sphenodon Güntheri*). *Trans. Proc. New Zealand Inst.*, vol. 10, pp. 222-239.
- OMAWA, G. 1898. Beiträge zur Anatomie der *Hatteria punctata*. *Arch. Mikros. Anat.*, Bd. 51, S. 481-691.
- RABL, C. 1916. Über der Muskeln und Nerven der Extremitäten von *Iguana tuberculata* Gray. *Anat. Hefte*, Bd. 53, S. 681-789.
- ROMER, A. S. 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. *Bull. Amer. Mus. Nat. Hist.*, vol. 46, pp. 517-606.
- . 1922. The comparison of mammalian and reptilian coracoids. *Anat. Rec.*, vol. 14, pp. 39-47.
- WILLISTON, S. W. 1914. The osteology of some American Permian vertebrates. *Journ. Geol.*, vol. 22, pp. 364-419.
- . 1925. The Osteology of the Reptiles. Harvard Univ. Press, 300 pp.
- ZITTEL, K. A. VON. 1932. Text Book of Paleontology, vol. 2, ed. 2, rev. by Woodward, A. S. Macmillan, London, 464 pp.



## THE HALOPHYTE PROBLEM IN THE LIGHT OF RECENT INVESTIGATIONS

By V. J. CHAPMAN B.A., PH.D., F.L.S.

*Late Frank Smart Student in Botany, Gonville and Caius College, Cambridge,  
Henry Fellow at Harvard, 1935-1936*

### INTRODUCTION

**D**URING the last few years considerable advances have been made in our knowledge of the conditions under which the halophytes exist. Until a short time ago the halophyte problem was approached purely from the morphological aspect, and there was no information available providing quantitative data about the environmental conditions and the physiological constitution of the different plants. Morphological investigation has shown that there is a considerable variation in structure among halophytes: there are the succulents, e.g. *Salicornia* spp.; grasses, some of which have salt-excreting glands, e.g. *Distichlis*; plants delicate in structure and which remain nearly always submerged, e.g. *Zostera*; and plants with no apparent special halo-combating mechanism, e.g. *Juncus Gerardii* and *Phragmites communis*. Some species that occur in haline communities also may be found in other habitats. *Phragmites communis* may be cited as an example occurring in fresh water and also on dunes (Voorne in Holland). A possible explanation in these cases may be the existence of different physiological races. This is a possibility that has not yet been examined but an autecological investigation should contribute to its elucidation.

In the last few years papers have appeared with a profusion of facts about the environmental conditions and physiological reactions of the halophytes of salt

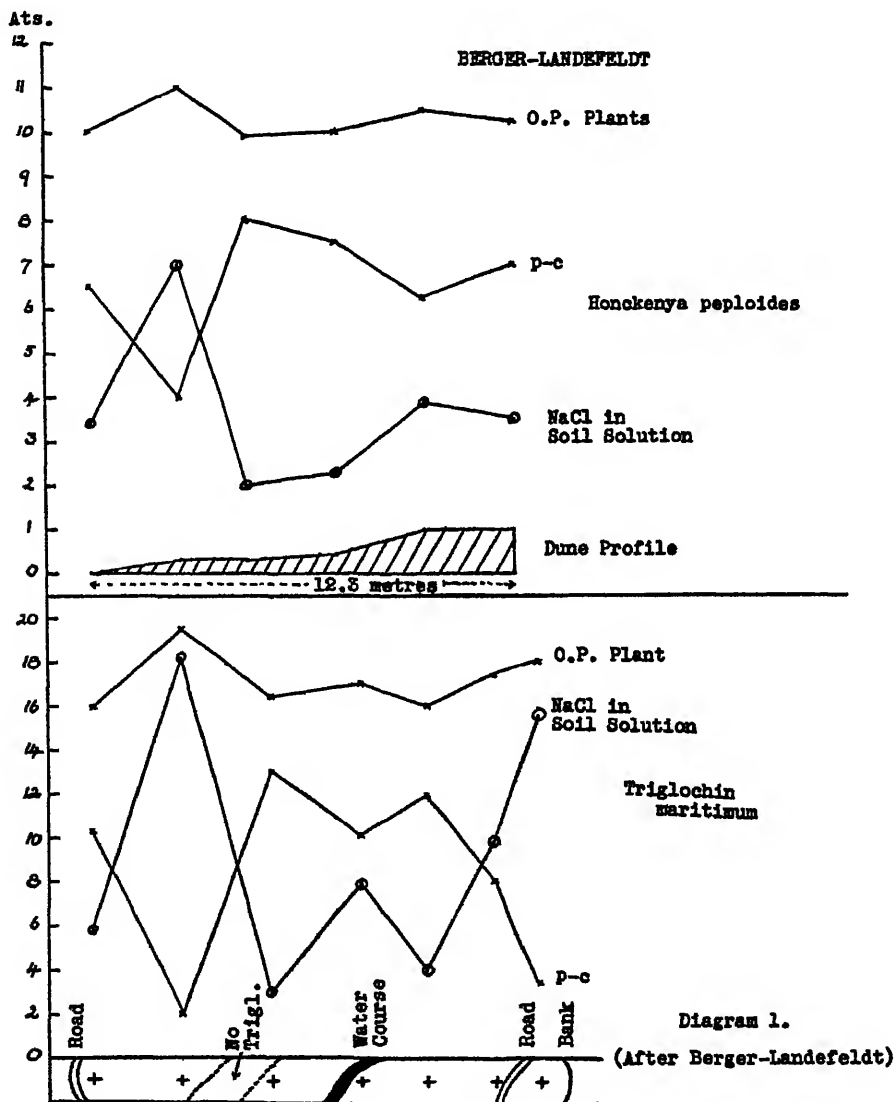
marshes and of the salt deserts. As a result of these papers a new outlook on the halophyte problem has been introduced, an outlook rendered valuable by the fact that it rests upon measurements made under field conditions or under conditions that approximate to those in the field. We are still a long way from complete knowledge of the why and wherefore of halophytes and it seems increasingly evident that future research must be a combination of autecology and physiology.

### HALOPHYTES AND SOIL SALINITY

The structure and existence of halophytes do not seem to be entirely separable from their actual distribution. Factors that influence the distribution by bringing about a physiological response from the plant must also be of importance to the general problem of halophytism. It has long been suggested that the distribution of halophytes is determined by the salt concentration of the soil solution, and therefore recent work along these lines should be of singular importance. In all these researches it is important to appreciate the fact that there is no adequate method of determining the absolute salt concentration of the soil. If the soil sample is leached with water and then titrated with silver nitrate there are at least two sources of error: one cannot be sure that all the chloride is removed by leaching as some may have been absorbed by the soil colloids; secondly, the result gives the total chloride content and pro-

vides no information about the metallic ion. To secure this information a separate analysis is necessary. In general, the bulk of the chloride can be regarded as sodium

been carried out chiefly on elementary organisms (e.g. *Dunaliella*) and it remains to be seen how far it will be applicable to the phanerogams.



chloride, but at the same time it is evident from recent work (cf. Baas-Becking [1]) that in some cases the metallic ion may be of importance. This work, however, has

#### a) Dune and salt marsh halophytes

Berger-Landefeldt [2] has recently investigated the changes of salinity that

occur in two communities, one dominated by *Triglochin maritimum* and the other by *Honckeya pyploides*. The other plants were disregarded and the study is especially valuable because it forms the basis of an autecological investigation which it is to be hoped will be continued. The principal results are shown in diagram 1 which is taken from the original paper. These results led Berger-Landefeldt to the conclusion that the osmotic pressure of the cell sap of these two halophytes is dependent upon the salt concentration of the soil solution, and it can be seen that the two curves follow each other fairly closely. This correlation, perhaps, is not surprising but it is important because it is a quantitative confirmation of a previous theoretical hypothesis. Although there may be this correlation between soil salt concentration and osmotic pressure of the sap, one still does not know how the former may operate in determining the existence (and hence distribution) of any halophyte: the salt concentration may be limiting either as regards its range or for a maximum or minimum value. This appears to be the deficiency of most of the recent investigations, because when the operation of a factor upon some species has been suggested the work ceases, and the autecological investigation of the application of the results to one or more species is never tried. Berger-Landefeldt, however, goes one step further along this line of enquiry. He investigates the values for  $p - c$ , where  $p$  = o.p. sap and  $c$  = o.p. soil solution. The significance of this function lies in the fact that when  $p - c$  is a maximum the cells are turgid, the plants are healthy and growth is good. When  $p - c = 0$  he suggests that the plants are at the condition usually termed the 'wilting point'. It will be seen from diagram 1 that the curve for  $p - c$  is the

antithesis of that for soil salt concentration and therefore has a negative correlation with it. What one would like to know next are the soil salt concentrations for different halophytes that produce for each species a value of 0 for  $p - c$ . This will be an important value, not only in indicating one limiting factor for their distribution, but also it will have a definite physiological significance.

#### b) Chloride Changes in Salt-desert Soils

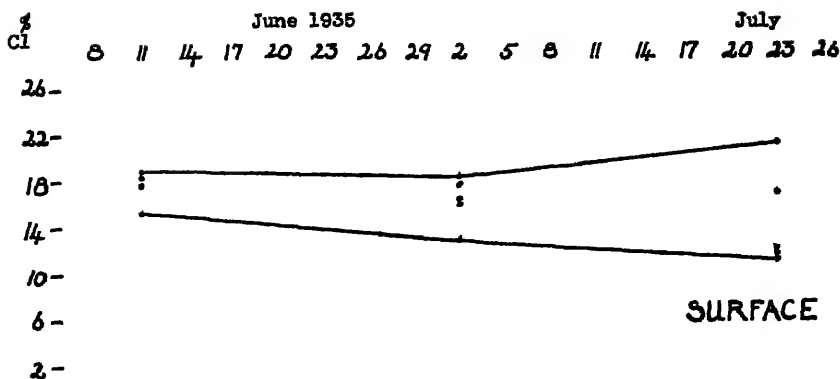
Adriani [3] has recently provided figures showing the changes of salinity during a summer for various communities in a French Mediterranean salt desert. He shows that for the surface soil the salt concentration increases in summer until salt crystallises out. A similar phenomenon can be seen on the east coast marshes of England where the bare ground and the leaves of *Limonium vulgare* may be covered with a salt deposit. The value of his work lies principally in showing the great range of salinity some plants can tolerate, and it suggests that in their case, perhaps, salinity is not such an important factor. In this work, as in other recent examples of field determinations, no indication is given as to sampling error. Work done by the present author has indicated that at least five samples (and preferably ten) should be taken from each community in order to provide an adequate idea of the possible variation. Diagram 2 illustrates the nature of the sampling error for salinity in an English salt marsh community.

#### c) Variations in salt concentration

Schratz [4] has carried out experiments upon certain halophytes by growing them in salt-solutions of varying concentrations. As a result of his experiments he has been able to show that by increasing



## THE QUARTERLY REVIEW OF BIOLOGY



Variations and Ranges in Salinity at Different Depths in a Plantagetum on the East Coast Salt Marshes of England.  
(To Indicate Nature of Sampling Error)

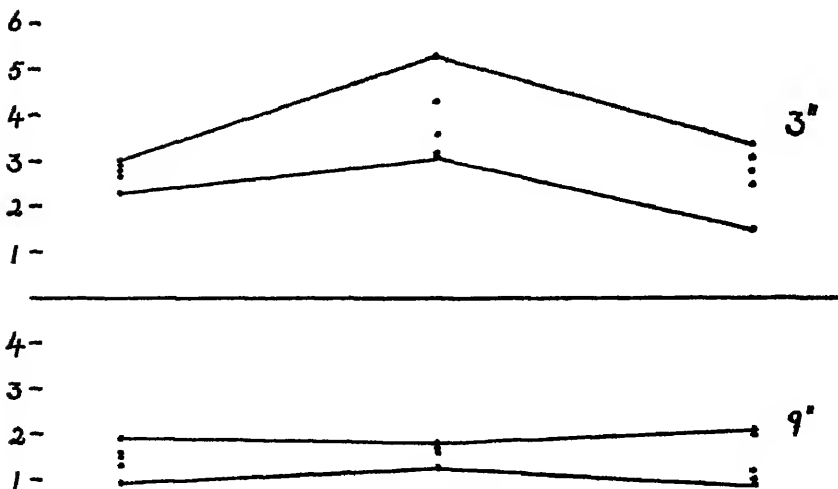


Diagram 2

the salt concentration from 0 per cent to 0.6 per cent

- (1) The total water consumption per fresh wt. is increased.
- (2) Transpiration per fresh wt. is lowered.
- (3) There is an increase in fresh wt. gain of the plant per unit period

of time. (0 — .3 per cent NaCl only.)

- (4) Productivity of the transpiration current is raised.

By this latter is meant

$$\frac{\text{Increase in fresh wt. of plant}}{\text{Total water uptake}}$$

Whether one is justified in regarding this ratio entirely as a product of the transpiration current is not argued. Diagram 5a, for *Plantago coronopus*, reproduced from Schratz's paper, shows the kind of results he obtained, and it will be noticed that the maximum difference in fresh wt. gain occurs at the flowering period. It is interesting to note that for fresh weight gain and productivity 0.6 per cent NaCl appears to have a depressant effect, and in this connection it must be pointed out that the salt concentrations used by Schratz are low compared with values which have been recorded from halophyte habitats elsewhere (the present author has recorded values up to 27 per cent, cf. below). One wishes, therefore, that the effects of still higher concentrations had been studied as giving a truer picture of the conditions under which halophytes exist. At present one does not know much about the behavior of the plants at higher chloride values. Schratz suggests that the chloride may operate upon halophytes in three ways:—

(1) Lowers the total water need by decreasing transpiration, reducing surface development and ultimately reducing the whole evaporating surface.

(2) Increasing fresh wt. gain by raising the productivity of the transpiration current. This holds good only for low values of NaCl. At the same time Schratz suggests that ecologically this is the most important effect, but again it must be stressed that his salt concentrations appear to be lower than those occurring naturally, and this fact tends to neutralise the importance of the suggestion.

(3) The salt taken in by the plant regulates the O.P. of the sap and also the acidity of the sap.

#### d) Early stages of development and salt concentrations

*Seed germination.*—Schratz [4] has tried the effect of different salt solutions on the germination of seeds of *Lepidium sativum*, *Senapis alba*, and *Aster tripolium*. The latter came from two habitats, one haline, the other non-haline. His results showed that there is no fundamental difference between the saline *Aster* and the others. The general effect at high concentrations (1.18 per cent salt, whereas Montfort has recorded 2.3 per cent for *Aster* and the present author 6.7 per cent) is to delay the start of germination, but once started it proceeds at a greater rate so that after about 17 days there is no marked difference in per cent germination with per cent salt concentration.

*Seedling development.* The effect of salt upon the development of seedlings of a few species was investigated by Montfort and Brandrup [5]. Their principal conclusions are summarised in the schematic diagram below. The optimum salt concentrations found for development were—

*Aster tripolium*: fresh water — .39 per cent salt

*Salicornia herbacea*: about 2.5 per cent salt

This investigation must be regarded as autecological and of great importance. It demonstrates that the salt concentration of the surface soil in the spring is a potent factor, and it suggests that this seasonal salt concentration may be one of the ultimate factors determining the distribution of these two species. It also indicates that seedlings may respond in a different way than the adult plants to the environmental factors. Montfort, for example, never records a salinity for *Aster* in the seed region of the soil lower than 0.52 per cent. This suggests that, in general, *Aster* seedlings do not germinate in nature

under optimum conditions. I have obtained some confirmation of these results by growing plants of *Aster tripolium* in salt marsh soil watered (a) with sea water (b) with fresh water and (c) in garden soil watered with fresh water. The plants did best in (c) and died in (a). The final salinities were (a) 18.63 per cent (b) 2.68 per cent (c) 1.47 per cent chloride.

These results show that an intensive study for a year of the habitat factors of *Aster* and *Salicornia* would probably yield extremely valuable results. In European salt marshes *Aster tripolium* usually occurs at low levels next to the *Salicornietum*, and

#### e) Maximum salinities

The following figures have been collected from various sources and serve to indicate the high concentrations that some species are capable of tolerating.

	% Chloride		
	Surface Max.	Min.	Root region
<i>Aster tripolium</i> .....	12.8	0.52	6.61
<i>Salicornia herbacea</i> .....	6.9	1.9	....
<i>Triglochin maritimum</i> ....	12.8	0.38	6.61
<i>Phragmites communis</i> ....	12.8	....	6.61
<i>Scirpus maritimus</i> .....	3.78	0.14	2.48
Bare ground.....	10.00	5.8	....

In addition, the present author has records of *Samolus valerandi*, *Phalaris arun-*

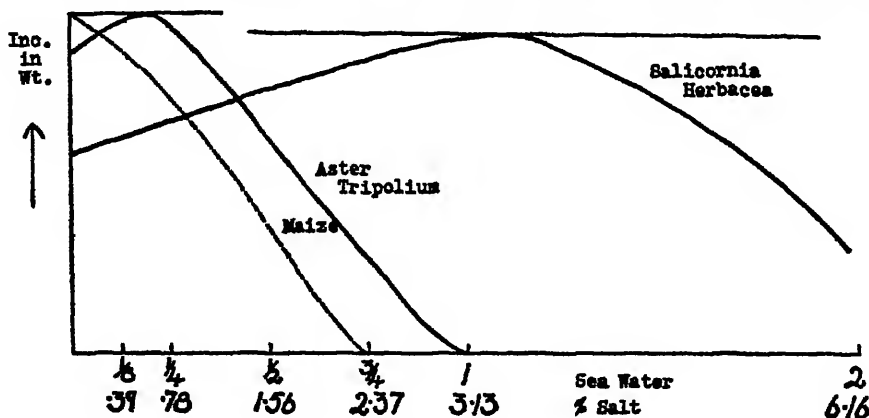


DIAGRAM 3 (After Montfort)

in view of the great differences in salinity toleration exhibited by *Aster* and *Salicornia* respectively a knowledge of any seasonal fluctuations in soil salinity appears important. It is extremely striking that a species such as *Aster*, which usually grows at low levels on salt marshes and is inundated by tides frequently, should show its optimum growth in fresh water conditions. It is by the investigation of such a species, growing in true haline conditions and yet flourishing best in a glycophytic medium, that one can hope for a considerable advance on our knowledge of halophytes.

*dinacea*, and *Oenothera pseudanifolia* growing in salt concentrations between 2 — 4 per cent.

#### HALOPHYTE HABITATS

As a result of his investigations into soil salt concentration in relation to different halophytes, Berger-Landefeldt [2] distinguished two types of halophyte habitat. The first he termed the xero-haline and the second the hygro-haline. The characteristics of the former habitat are that it is very dry, has a low salt concentration, and the plants have a low osmotic pressure and usually possess deep

roots. One of the principal difficulties would appear to be to determine that salt concentration at which any given habitat becomes haline, and it might be legitimate to ask whether the xero-haline habitat really should be regarded as truly haline. The hygro-haline habitat is moist or very wet and has a high salt-concentration. There is usually a ready flow of salt water and the plants are typified by comparatively high osmotic pressures, 15-20 atmos. This classification of halophyte habitats is used also by Steiner [6] who considers subdivisions of the hygro-haline type which will be referred to later. It is probably too early yet to say how far this division is going to be satisfactory and much more data are required. If the generalisations of Berger-Landefeldt hold good then it seems as if we have been provided with a real contribution towards the halophyte problem. Autecological studies of hygro-haline and xero-haline plants should lead to a much better understanding of the general halophyte problem.

#### OSMOTIC RELATIONSHIPS OF HALOPHYTES

##### a) Osmotic pressure of Surface Soil

Steiner [6] has recently investigated the relation of the distribution of salt marsh vegetation to osmotic pressure of the soil. He found that it varied over short distances horizontally and these variations could be correlated with the distribution of the dominant species. The type of result he got is depicted in diagram 4.

In connection with these results, however, it is necessary to point out certain facts. Although the soil osmotic pressure may show these variations, at the same time one cannot say it is due to any one salt in the soil. The cryoscopic method of determination employed involves all the soluble salts in the soil solution and one does not know which is the dominant

component. It would be interesting to have had the figures for chloride concentration for comparison. Further, Steiner's paper gives no clear indication of the sampling error. This may be considerable and it has already been shown that the chloride range tolerated by one species may be very wide, and unless there is any compensating action by the other solutes then the O.P. of the soil would also vary.

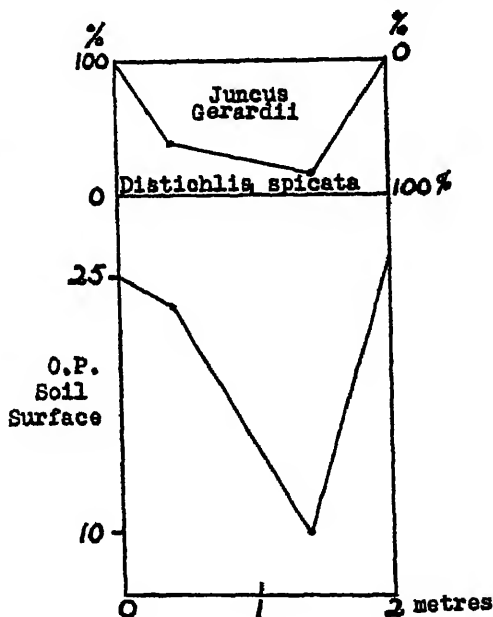


Diagram 4  
(After Steiner)

Unless one knows the maximum range of the O.P. in a given area one cannot tell whether the observed fluctuations have any significance or not. Steiner's results are full of interest but their interpretation requires caution in view of these possibilities.

##### b) Changes of O.P. with depth

This information is also provided by Steiner and must be subject to the limita-

tions already mentioned. The curves for *Distichlis spicata* and *Spartina glabra* are similar to those reproduced for *Salicornia mucronata* (diagram 5b). The other four species investigated showed little change with depth and had low O.P. values

the autumn rains (Curve 20 viii). *Spartina glabra* and *Distichlis spicata* behave similarly, whilst the other species (*Juncus Gerardii*, *Spartina patens*, *Salicornia herbacea*, and *Iva oraria*) show little or no change with season. The leaching effect

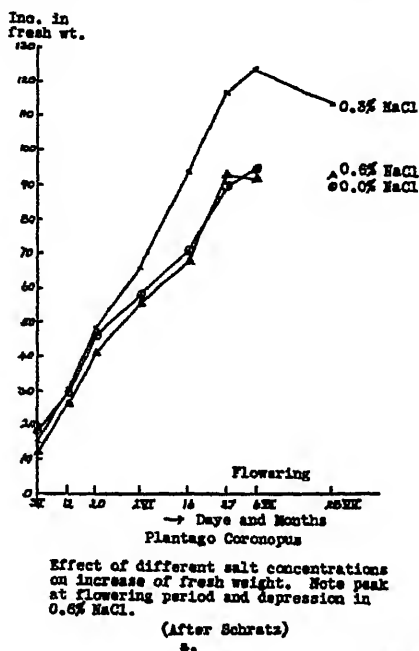
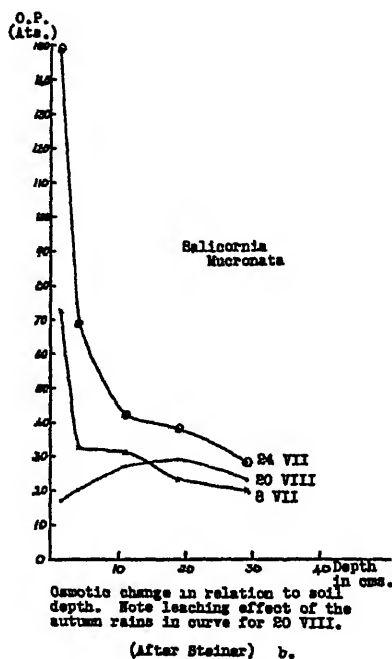


Diagram 5



throughout. If it were not for the inherent sampling error one might suggest that these four species are intolerant towards high osmotic pressure or great variations in osmotic pressure of the soil solution. The habitat of *Salicornia mucronata* shows the most extreme ranges and the tolerance of this species to such conditions suggests why it is a successful pioneer. The same applies to *Spartina glabra* and *Distichlis*, but to a lesser extent as their range is not so great.

### c) Variations in O.P. of the soil

The changes of the *Salicornia mucronata* habitat are shown in diagram 5b reproduced from Steiner's paper. This shows the great variation and also the effect of

of rain is also shown by the following set of figures.

Species habitat	O.P. in atm.	
	24 VI (before rain)	2 VII (after rain)
<i>Spartina glabra</i> .....	33.5	28.5
<i>Spartina patens</i> .....	25	21
<i>Distichlis spicata</i> .....	22	16.7
<i>Juncus Gerardii</i> .....	18.9	6.7
<i>Salicornia europaea</i> .....	40-45	4.3

Diurnal changes are provided by the following figures:—

Time	<i>Salicornia herbacea</i>	<i>Distichlis</i>	<i>Spartina patens</i>	<i>Juncus Gerardii</i>
8.30	149.4	106.8	31.1	28.7
17.40	198.0	155.0	39.1	28.8

In both these sets of figures no allowance appears to have been made for the sampling error nor can one tell which of the soil

salts had changed most in concentration. It is possible that the diurnal changes are covered by the sampling error. What one would really like to know is the maximum change that can occur in one day during any part of the year. It is also probable that the maximum and minimum values are of more significance than the daily change.

In addition to the changes described above, Steiner says that temperature and hour after flooding (salt marsh) also affect the O.P. of the soil, but he does not provide any figures or give any indication of the value of the variations.

#### d) Osmotic pressure of cell sap and soil

Adriani [3] has declared that the osmotic pressure of cell sap is higher for plants living in the more saline soils, and that it can also be correlated with the salt content of the soil. The greatest range found in the Mediterranean was shown by *Obione portulacoides*, 22-105 Atmos. In this connection it must be pointed out that a correlation between O.P. cell sap and the salt content of the soil should depend upon the relative proportion of NaCl in the soil in relation to the other soluble salts.

#### e) Variations in O.P. cell sap of the Halophytes

When the variations in O.P. of the sap are investigated during the growing season it is found (Steiner) that the halophytes can be grouped into three classes depending on their behavior.

I. O.P. cell sap fluctuates with rainfall. In dry weather the O.P. rises and in wet weather it falls. This is shown in diagram 6I, where *Spartina glabra* is a typical example.

II. The alterations in O.P. sap are, in general, an expression of displacements in water content. The changes reflect those

of all the O.P. components and not that of  $\text{Cl}^-$  only as in group I. *Solidago sempervirens* is an example. (Cf. diagram 6II.)

III. There is no relation to the external conditions. The O.P. shows a relation with the  $\text{Na}^+$  and  $\text{Cl}^-$  components and the salt taken in forms the controlling mechanism. The best example of this group is *Juncus Gerardii*. (Cf. diagram 6III.)

#### MAXIMUM OSMOTIC PRESSURES

Steiner has measured the O.P. of the cell sap of a large number of species and he has shown that the osmotic pressures may vary from 13-48 atmospheres. The O.P. cell sap is due to the soluble salts contained in it and from his figures it can be seen that the NaCl component may vary from 18-85 per cent of the total O.P. This makes it all the more important to know the percentage effect of the different components that determine not only the cell sap O.P. but also the soil solution O.P. Unfortunately Steiner has not given any figures for the components of the soil solution O.P. and this materially decreases their value. He also indicates by his figures that the Sodium component for the cell sap may be greater than can be accounted for by the chloride. In the case of *Spartina glabra* the  $\text{Na}^+$  component accounts for 25 Ats. of the total and the chloride for only 17 Ats. (Cf. also diagram 6IV).

The following table indicates the maximum values for the soil solution O.P. and also the range of variation.

Species	Surface (Atm.)		Root (Atm.)	
	Max. value	Variation	Max. value	Variation
<i>Salicornia mucronata</i>	198	182	60	30-40
<i>Spartina glabra</i> ....	147	130-25	29	2
<i>Distichlis spicata</i> ..	155	72- 7	24	3- 2
<i>Spartina patens</i> ....	31	18-10	21	1
<i>Juncus Gerardii</i> ....	29	17- 6	24	3- 1
<i>Hemkya peploides</i> ..	10.88	11	..	....
<i>Triglochin maritimum</i>	19.64	3- 7	..	....

From these figures it is clear that *Juncus Gerardii* and *Spartina patens* differ from the other three in the surface conditions but when the root area is concerned it is *Salicornia mucronata* that differs from the rest. Biologically, changes in the root region will be more important and hence more significant.

	Soil. 0-1 cm.	Sap.
Shaded.....	60 2 Ats.	53 9 Ats.
Partly Shaded.....	58 9 Ats.	27 3 Ats.
Unshaded.....	42 1 Ats.	32 3 Ats.

This suggests a correlation between soil and sap O.P. but it must be remembered that no allowance is made for sampling error, so that there is no indication of the

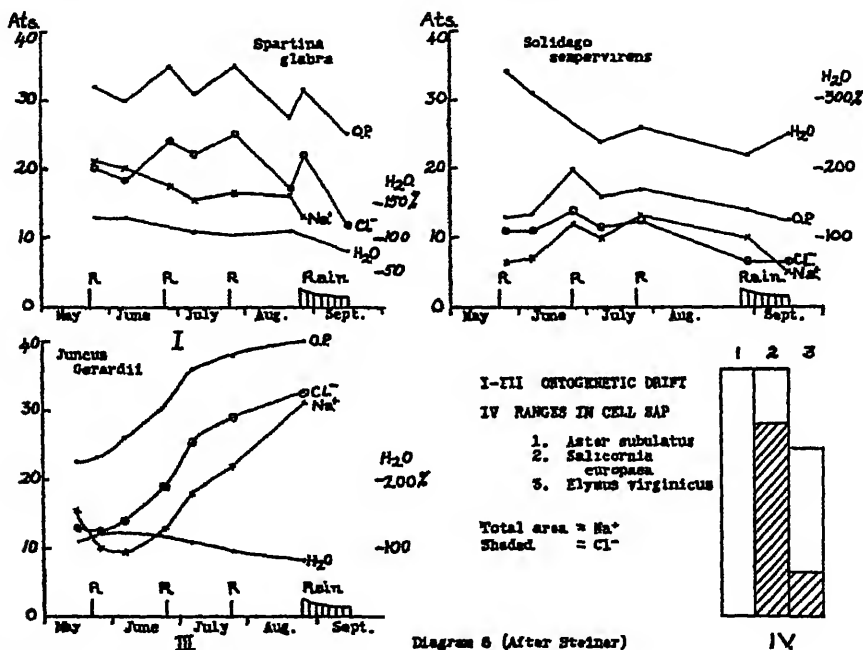


Diagram 6. There are 3 groups ontogenetically:—

- I. O. P. shrinks with rainfall. Dry means a rise; wet means a fall.
- II. The trivial alterations in O. P. are, in general, an expression of displacements in water content. Changes in O. P. reflect those of all components.
- III. No relation with weather. There is a definite relation with NaCl content, and the salt taken in is the controlling mechanism.

#### SALICORNIA HERBACEA

It has been suggested earlier that autecological studies of one or two halophytes might lead to useful conclusions. In support of this thesis a short survey will be made of the known facts relating to the so-called *Salicornia herbacea*, such facts being gathered from a number of recent papers. Steiner [6] has obtained some figures for the osmotic pressure relations.

possible range under the different conditions. Steiner concludes that the optimal development is inhibited in a habitat poor in salt, whilst a very high salt content produces a stumpy form and may cause death. He further concludes that the optimum development of the species is determined by the light value. In 1915 Johnson and York [7] suggested that at high levels soil moisture content determined the existence of the plant whilst at

low levels length of submergence was the dominating factor. This idea has been carried a stage further by Wiehe [8] who has shown that under certain physiographic conditions submergence may act mechanically at low levels by uprooting the seedlings.

Wiehe does not, however, provide any data about salinity changes etc. but at the same time his work suggests that *Salicornia* might exist under certain conditions but that it is prevented from doing so by mechanical forces. Work by the present author (unpublished) on salt marshes of east England leads one to conclude that submergence may be an important factor, but that other factors are probably involved as well. Montfort and Brandrup [5] have shown that the salinity for optimum development is 2.5 per cent whilst the range for the species appears to be between 6.9 per cent and 1.9 per cent. From a survey of the various papers a list of the principal factors which appear to influence the growth and distribution of this species can be drawn up:

- a) Number of submergences
- b) Length of non-tidal exposure (a period of one or more days during which no tide covers the area)
- c) Salinity
- d) Soil moisture
- e) Competition.

Although all these suggestions have been made by various authors it is to be regretted that no field experiments have been carried out to prove these hypotheses. One of the objects of this survey is to show that there is plenty of information but that it wants collating for each species, and then a series of field experiments devised and carried out to prove the various suggestions.

#### OSMOTIC VEGETATION OF HYGRO-HALINE HALOPHYTES

As a result of his observations on osmotic pressure Steiner [6] has suggested that there are three types of regulatory mechanism for O.P. of hygro-haline halophytes.

I. Succulence. Their osmotic changes are compensatory. When there is an increase in the salt content of the sap there will be a dilution from the water store, e.g. *Iva ovata*, *Plantago maritima*, *Salicornia* spp.

II. 'Absalzende' forms. There is no permanent rise in the O.P. because any salt accumulation is controlled by the salt removing glands. Examples:—*Spartina* and *Distichlis*.

III. No regulatory mechanism. The maximum peak of the O.P. rise marks the end of the vegetative period. e.g. *Juncus Gerardi*.

In the light of these conclusions the structure of halophytes takes on a new interest and their morphological characters assume a physiological significance.

#### CONCLUSION

The results of recent researches indicate that the halophyte problem is concerned with a number of environmental factors. Future investigations, it would seem, must be concerned with how and when these factors operate. It is necessary to know which season of the year is vital and which part of the plant life cycle is most affected, and what particular organ of the plant receives the stimulus. It is also essential to have information concerning the greatest range for a factor that any given species can tolerate. Finally such conclusions as are reached require to be tested by field experiments, which up to the present have not been numerous. Finally,



it cannot be stressed too strongly that autecological studies of different halophytes combined with physiological experiments, would probably lead to considerable advances in our knowledge of their behavior and mechanism.

## LITERATURE

1. BAAS-BECKING, L. G. Report of VIth Int. Bot. Cong. *Amsterdam*, 1935.
2. BERGER-LANDEFELD, U. Die Hydratur einiger Halophyten in ihrer Abhängigkeit von der Substrat-Konzentration. *Bei. Bot. Cent.*, Vol. 51.
3. ADRIANI, E. D. Preliminary report on an ecological survey of the salt deserts of the Mediterranean. *Bull. Montpellier Biological Station*, 1935.
4. SCHRATZ, E. Beiträge zur Biologie der Halophyten. *Wiss. für Bot.*, 1934.
5. MONTFORT, C., AND BRANDRUP, W. Physiologische und pflanzengeographische Seesalzwirkungen. *Wiss. für Bot.*, 1927, 1928.
6. STRINER, M. Zur Oekologie der Salzmarschen der Nordöstlichen Vereinigten Staaten von Nordamerika. *Wiss. für Bot.*, 1934.
7. JOHNSON, D. S., AND YORK, H. S. The Relation of Plants to Tide Levels. *Corn. Inst. Pub. Washington*, 1915.
8. WIEBE, P. O. A quantitative study of the influence of tide upon populations of *Salicornia europaea*. *Journ. of Ecology*, 1935.





## NEW BIOLOGICAL BOOKS

*The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.*

### BRIEF NOTICES

#### EVOLUTION

RACE, SEX, AND ENVIRONMENT. *A Study of Mineral Deficiency in Human Evolution.* By J. R. de la H. Maret. Hutchinson and Co., London. 21 shillings net. 9 x 6; 342; 1936.

An interesting theory of human evolution. The author's conception is that mineral deficiencies of the soil and the resulting vegetable food have influenced animal and human evolution. Chapter I deals with the general problem. The next four chapters "contain some of the more important ecological and physiological facts that are intended to supply means for the formulating and checking of the theories of physical and social evolution constituting the remainder of the book. This main object is to trace the distribution of the more important minerals, together with their effects outside the human body; and in particular to determine which of them are abundant and which rare as a result either of aridity or of humid conditions." An attempt is then made to envisage the kind of physiology best suited to each special environment. In the remaining eleven chapters the theories presented are applied to the problem of human evolution. The author believes that mineral deficiency has influenced selection both for bodily and for mental characters, some of which appear to have become linked even before the emergence of the vertebrate on to the land. Considerable space is given to a discussion of the origin of man, also to a hypothesis whereby mineral deficiency

is credited with the power of removing or simplifying characters whose over-specialization might otherwise have prevented further and alternative adaptation. Mineral deficiency is also held responsible for a series of arrests of bodily growth, during each of which the relative size of the brain to the body has been increased.

The author confesses that his researches have raised many more questions than he has been able to answer. These enter not only the domain of the anthropologist but that of the geologist, the soil chemist, the geneticist, the physiologist and the psychologist. All workers in these fields will find this a stimulating book. It is documented and contains a glossary, and an author's and subject index.

ÉVOLUTION DE L'ATMOSPÈRE. *Circulation Organique, Époques Glaciaires. Actualités Scientifiques et Industrielles* 271. *Exposés de Biométrie et de Statistique Biologique*, VIII.

By V. A. Kostiçin. Hermann et Cie, Paris. 10 x 6½; 46; 1935 (paper).

This is an attempt to express in a generalized mathematical form the variations in the quantity of oxygen, carbon (CO<sub>2</sub>) and nitrogen present on the earth; and the relation of these variations to vital phenomena. A system of differential equations is used to represent the interchange of the above elements between the atmosphere, lithosphere and hydrosphere and in relation to the metabolism of plants and

animals. The equations are simple and their characteristics are briefly analyzed. The author proceeds then to re-examine the hypothesis of Arrhenius regarding the origin of the glacial periods. As it is recalled, Arrhenius attributed the appearance and disappearance of glacial periods to the changes in the quantity of atmospheric CO<sub>2</sub>. Our author overcomes the numerous objections to the hypothesis of Arrhenius by extending his equations to include variations in the activity of volcanoes and in the vertical movement of the earth's surface. The resultant equation, according to the author, satisfies the requirements necessary to explain the localization and periodicity of glaciation.

As the author admits, this is only a first approach to the mathematical analysis of the variations of the three elements and of the consequences of these changes. It will be interesting to note at what less generalized derivations the method will arrive.



#### L'Espèce.

By L. Cuenot. *Gaston Doin et Cie, Paris.*  
30 francs. 8 $\frac{3}{4}$  x 6; 310; 1936 (paper).

To the age old question—What is a species?—the eminent French biologist seeks an answer by enlisting the aid of modern genetics. He first re-examines the classical definition and traces its historical origin, then discusses the terminology introduced by the modern taxonomists. After a concise and clear exposition of the principles of genetics, the author describes the morphologic and physiologic characteristics, the genetic constitution and the ecology of some 30 "species" of plants and animals. With the emphasis on the genetic characteristics, he discusses and criticizes the basis of the classification given the "species" in question. From these and other general considerations he concludes that the classical definition of species enables the systematist to group most varieties of plants and animals. For the remainder, he proposes some general rules which he illustrates with concrete examples. From this study, it becomes evident that we are yet far away from a classification which can be consistent and

objective. Teleologic concepts still persist and apparently there are some who find it difficult to differentiate between the object and its name. The author's critical analysis should contribute much towards a more precise terminology.



VÉRIFICATIONS EXPÉRIMENTALES DE LA THÉORIE MATHÉMATIQUE DE LA LUTTE POUR LA VIE. *Actualités Scientifiques et Industrielles*, 277. *Exposés de Biométrie et de Statistique Biologique*, IX.

By G. F. Gause. *Hermann et Cie, Paris.*  
18 francs. 10 x 6 $\frac{1}{2}$ ; 63; 1935 (paper).

This small volume can be looked upon as an extension and experimental elaboration of certain of the ideas developed by Doctor Gause in his recent book, *The Struggle for Existence* (reviewed in Q. R. B. June 1935). In the present volume the author discusses the following three types of biological associations: first, the competition between two species in the same ecological niche for the same food; second, the competition between two species in different ecological niches for the same food, and, third, the predator-prey situation where one species lives at the expense of the other. The experiments illustrating the first relationship are based on competitions between *Paramecium aurelia* and *P. caudatum*; the second relationship is illustrated with *P. caudatum* and *P. bursaria*, and the third with *P. bursaria* (predator) and *Saccharomyces exiguus* (prey).

This book forms an interesting addition to the field of experimental populations although it does not add greatly to the theoretical ideas developed by the author in his earlier volume; in fact it should be used as an appendix to the latter work. There is a brief bibliography and several text illustrations.



EINFÜHRUNG IN DIE PALÄONTOLOGIE.

By Hermann Schmidt. *Ferdinand Enke, Stuttgart.* 15 marks (paper); 16.80 marks (cloth). 10 x 6 $\frac{1}{2}$ ; 253; 1935.

An introduction to paleontology with chapters devoted to the animal forms in

ascending order, followed by a chapter on plants and three others treating paleobiology, biostratigraphy and methodology, respectively. A short bibliography of selected titles and an index of animal and plant names are included. A good textbook, whose usefulness, however, will be largely confined to German schools.



ENVIRONMENT OF THE EARLY VERTEBRATES, by Alfred S. Romer and Brandon H. Grove. SUMMARY OF UPPER DEVONIAN STRATIGRAPHY, by George H. Chadwick.

*American Midland Naturalist*, University of Notre Dame, Notre Dame, Indiana. 30 cents. 9 x 6; 57; 1935 (paper).

The major portion of this treatise is devoted to a description and summarization of habitats of early vertebrates found in North American pre-Carboniferous material. For purposes of study the investigator groups the various finds into four classes, 1-4, in order of their gradation from fresh to salt water conditions of deposition. Conclusions derived from analysis of this material unquestionably indicate that fish history commences in fresh waters.



BULLETIN OF THE BUFFALO SOCIETY OF NATURAL SCIENCES, Volume XVII, No. 1. *New Fossils from the Western New York Devonian*. Containing following articles: *Some New Forms and New Occurrences of Fossil Plants from the Middle and Upper Devonian of New York State*, by Chester A. Arnold; *Pseudobryozoa, a New Hamilton Dictyosponge*, by Irving G. Reimann; *New Upper Devonian Fishes from Western New York*, by William L. Bryant; *New Species and Some New Occurrences of Middle Devonian Blastoids*, by Irving G. Reimann.

*Buffalo Society of Natural Sciences, Buffalo.* 9½ x 6½; 45 + 4 plates; 1935 (paper).



## GENETICS

THE BEGINNINGS OF PLANT HYBRIDIZATION  
By Conway Zirkle. *University of Pennsyl-*

*vania Press, Philadelphia.* \$2.50. 9 x 6; xiii + 231 + 8 plates; 1935.

Unfortunately, in the brief space allotted, it is only possible to indicate a few of the many interesting features of this book. The author has made a painstaking investigation of all the known literature pertaining to plant hybridization before Koelreuter. A brief survey of ancient and medieval beliefs concerning hybridization is given, concluding with John Ray who in his sermon on natural theology about 1660 anticipated Darwin's pangenesis hypothesis and described alternate or Mendelian inheritance of human hair color. The first real intimation that hybrid plants could be secured by cross pollinations seems to have come from Camerarius. In this country the Indians long recognized the tendency of different types of maize to mix. The author quotes in full from the original sources of the early descriptions of xenia and gives a reproduction of the earliest Mendelian segregation as illustrated by Jakob Theodor of Berg-zabern (Tabernaemontanus).

Accurate accounts of plant hybridization date from the first half of the eighteenth century. The first record is by Cotton Mather in 1716, then follow such names as Thomas Fairchild, Richard Bradley, Jean Marchant, Thomas Knowlton, Philip Miller, Paul Dudley, and many others, down to and including Linnaeus. Of the utmost importance to the reader will be the reprinting, usually in full, of the original writings of these men. In the final chapter is given a résumé of later hybridization. The volume contains a number of illustrations, a lengthy bibliography and a detailed index.



GENETIC VARIATIONS IN RELATION TO EVOLUTION. *A Critical Inquiry into the Observed Types of Inherited Variation, in Relation to Evolutionary Change.*

By H. S. Jennings. *Princeton University Press, Princeton, N. J.* \$2.00. 8½ x 5½; iv + 139; 1935.

This volume is based on a series of lectures given at Princeton University in 1934. The topics discussed in the five lectures are as follows: I. Structure of the germ

plasm. Genetic variations resulting from new combinations of genes; II. (1) Genetic variations resulting from irregularities in the structure and operation of the genetic system. (2.) Gene mutations; III. Are the gene mutations observed in experimental genetics the basic material of progressive evolution?; IV. Genetic variation in unicellular organisms, with special relation to the inheritance of environmental effects and reactions; V. Genetic variation in unicellular organisms, continued. What is the method of operation of the genetic system in bringing about genetic variations under the long-continued action of environmental conditions? A book of interest to all biological students and teachers of biology in universities, colleges, and secondary schools. It is illustrated and to each chapter is appended a series of notes and references. There is no index.



LES CONCEPTIONS MODERNES DE L'HÉRÉDITÉ  
By Maurice Caullery. Ernest Flammarion,  
Paris. 15 francs. 7½ x 5; 312; 1935  
(paper).

This is an unusually clear exposition of the fundamentals of genetics. The author summarizes the most important investigations on the subject, both experimental and statistical, and interprets the findings in terms understandable by the layman. Very little is omitted and in fact this little volume is more comprehensive than many a textbook. A noteworthy feature is the excellent perspective of the author in evaluating the contribution of each geneticist. While the work on Mendelian inheritance receives the most attention, yet the author has not neglected the non-Mendelian forms. The bibliography is sufficient.



#### GENERAL BIOLOGY

TRANSACTIONS OF THE BOSE RESEARCH  
INSTITUTE, CALCUTTA. Vol. IX, 1933-  
1934. *Biological and Physical Researches.*  
Edited by Sir Jagadis Chunder Bose. Long-  
mans, Green and Co., New York. \$7.20.  
8½ x 5½; iv + 210; 1935.

This volume deals with the following biological subjects. I. Modification of vital activity after inflorescence in *Mimosa pudica*, by S. C. Das and B. K. Palit. The appearance of inflorescence induces a depression of moto-excitability of the pulvinus. The velocity of excitatory impulse in the petiole of the leaf also undergoes appropriate variation at inflorescence. II. Periodic variation in longitudinal and diametric growth of stem in *Helianthus*, by S. C. Das and B. K. Palit. Special devices are described which give automatic records of the simultaneous variation of both longitudinal and diametric growths throughout a complete cycle. The results are given in detail. III. Automatic record of embryonic growth on germination of the seed, by B. K. Dutt and A. Guha-Thakurta. By means of the automatic apparatus herein described the actual moment of germination inside the seed of *Cicer arietinum* is determined; also the rate of growth of the embryonic radicle. IV. An automatic respiograph, by A. Guha-Thakurta and B. K. Dutt. The apparatus, constructed on the principle of the photosynthetic bubbler, automatically records the rate of oxygen consumption for respiration. V. A chemical, physicochemical and physiological investigation on oil soluble vitamins in *Cicer arietinum*, by N. C. Nag and H. N. Banerjee. Kabuli chhola oil supplies all the necessary essentials for proper nutrition, healthy growth, and propagation of rat colonies. In regard to oil-soluble vitamins, Kabuli chhola, closely followed by Shona moog, is superior to all other pulses. It approaches in vitamin efficiency cod liver oil. VI. An investigation on specific bacterial action on *Gur* solution unattended by evolution of carbon dioxide, by J. P. Sircar. "From the experiments given in detail it would appear that there are certain organisms which directly produce, in *Gur* solution, acetic acid, lactic acid, formic acid and acetone without evolution of any gas." VII. The racial affinities of the Oraons, by Provash Chandra Basu. This paper reports investigations on skin color, stature and head measurements of 250 primitive Oraons (adult males) living in the north-western plateau of the Ranchi district. A brief summary of their totems

is given. Detailed measurements of four male Oraon crania in the Anthropological Laboratory of the Zoological Survey of India are also included in the study. The volume also reports investigations that have been made on the continuous spectra of hydrogen halides and of the flame spectrum of hydrogen. Each paper is documented. There is no index.



ESSAI POUR UNE CONCEPTION PHYSIQUE DE LA VIE.

By D. Caléwaert. *Librairie Maloine, Paris.* 7½ x 5½; 78; 1935 (paper).

This is an attempt to explain life—its origin, and biological, physiological and chemical processes—in terms of physics. According to the author the first stage in the formation of matter was the impregnation of amorphous rocks by water (formation of the crystalline state resulting in ionization) and the fifth the impregnation of amino acids by methane (the formation of the polypeptides culminating in the higher organisms).

Caléwaert alleges that all matter depends for its survival on its molecular density. As measured by sera of blood, gastric juice, saliva and other secretions, a young body has a greater density than an old one, and growing older is a process of dedensification. Thus a child has a greater density than an adult, and the female (because of the additional secretions connected with lactation and menstruation) a greater one than the male. Disease occurs when the infecting organism has a greater density than the affected, and therefore physicians do well to include the administration of chemical extracts of compounds of high molecular weight in the treatment, thereby increasing the density of the sera of the affected body. By way of example, syphilis is dealt with in detail, although tumors, fevers, pregnancy and immunity are also treated. We like particularly the opening sentence of the chapter on pregnancy: "Pregnancy is a benign tumor since it is finally expelled from the maternal organism." The book is without index, but it does not need one.

COLD SPRING HARBOR SYMPOSIA ON QUANTITATIVE BIOLOGY. *Volume III.*

*The Biological Laboratory, Cold Spring Harbor, Long Island, N. Y.* \$3.75. 10½ x 7½; xv + 359; 1935.

The Cold Spring Harbor symposium for 1935 was built around the general problem of the influence of light on biological phenomena. The present volume, as with the previous two (reviewed in Q. R. B. 9: p. 369 and 10: p. 344), contains the papers given by the various selected investigators on this subject at Cold Spring Harbor. The discussions following each paper, which incidentally are frequently quite extended and illuminating, are included as before in the text of the volume. Such topics as the physics of light, the kinetics of photochemical reactions, the physiology of chlorophyll, the photosynthesis phenomenon, the influence of light on behavior responses, and the effect of light on metabolism are discussed.

This volume seems to be living up to the high standard of excellence set by its predecessors and should be in the hands of the biologist interested in light processes. Many of the articles are illustrated and contain an extended bibliography.



RELIGION AND THE SCIENCE OF LIFE. *With Other Essays on Allied Topics.*

By William McDougall. *Duke University Press, Durham, N. C.* \$3.00. 7½ x 5; xiii + 263; no date.

In the title essay of this volume Professor McDougall traces the lines of evidence that have led him from agnosticism to religion. The purposive activities of organisms, the logical and esthetic powers of the human mind, and the results of psychical research indicate to him "that each man is not what to so many scientists he has seemed to be, a fortuitous concatenation of physical forces, but is rather a ripple of the mighty ocean of spirit, an individualized ripple, small and feeble, yet sharing in the nature of the whole and not wholly detached from it." Other essays deal *inter alia* with the need for psychical research, family allowances as a eugenic measure, and the author's experi-

ments on the transmission of acquired characters.



#### DESERTS ON THE MARCH.

By Paul B. Sears. *University of Oklahoma Press, Norman.* \$2.50. 7½ x 5½; 231; 1935.

The author, who is now Director of the Department of Botany at the University of Oklahoma, has long been a student of the conservation of our natural resources. He has written, for the general reader, a history of the pillage and destruction in this country of our most valuable possessions—our soils, our vegetation, and our wild animal life. Not one particular class, but by and large all have been blindly doing their best, in one way or another, to wreck the balance between soil and plants and animals that had been established for centuries before the influx of the European, and had made for such an abundantly rich region. Professor Sears indicates how, by intelligent action, it is still possible to arrest the development of infertile soils, of deserts, and of arid streams. The book deserves to be widely read. It is without an index.



#### THE CHEMICAL CONTROL OF CONCEPTION.

By John R. Baker, with a Chapter by H. M. Carleton. *Chapman and Hall, London.* 15 shillings net. 8½ x 5½; x + 173 + 8 plates; 1935.

This is the definitive statement of the results of a series of experimental investigations on the action of various pure chemical substances and proprietary preparations as spermicides *in vitro*. Aside from practical considerations in the development of better contraceptive agents than those now available, in which the author evidently achieved a considerable measure of success, the chief interest of the book is in the critical methodology and techniques developed for the study of the physiology of spermatozoa. It is a valuable reference work for the biologist, well indexed.

#### THE JOURNAL OF BIOLOGICAL EDUCATION, Vol. 1, No. 1.

Edited by Isador Ripps. *Scientific Staff: M. Jay Chasin, V. Lewitus, N. R. Lubowe, L. Ripps, J. Washon, C. Weinrib, Speiss and Washon, New York.* 10 cents. 9½ x 6½; 32; 1935 (paper).

This little journal recently made its bow to the public with the aim of furthering the knowledge of and interest in the biological sciences. It deals briefly and simply with a wide range of subjects, such as notes on the early history of the microscope, the sea-horse, narcotic drugs and their action, health chats, etc., etc. Some of the articles are illustrated. The journal will find its chief readers among high school students and the general reader interested in all kinds of biological information.



#### URDEUTSCHLAND. *Deutschlands Naturschutzgebiete in Wort und Bild. Lieferungen* 13, 14.

By Walther Schoenichen. *J. Neumann, Neudamm.* 2 marks each. 10½ x 8½; Lief. 13, 1-24 + 9 plates; Lief. 14, 25-48 + 9 plates; 1935 (paper).

These two numbers inaugurate the second volume of a beautifully illustrated work treating of the nature conservation areas of Germany. This volume will be confined to the flora and fauna. The numbers comprising the first volume, on geology, have been noticed in the previous numbers of this REVIEW, beginning with Volume 10, Number 3.



#### ECOLOGICAL ASPECTS OF A CALIFORNIA ESTUARY.

By G. E. MacGinitie. *The University Press, Notre Dame, Ind.* 9 x 6; 136; 1935 (paper).

This paper presents an interesting description of a typical marine estuary of California located at Monterey Bay. The physical and biotic factors are discussed but a more valuable contribution is found in the fine catalogue of the animals with detailed natural history observations.

TRAVAUX DU LABORATOIRE DE MICROBIOLOGIE de la Faculté de Pharmacie de Nancy. Fascicule VIII.

Laboratoire de Microbiologie de la Faculté de Pharmacie de Nancy. 9½ x 6½; 117; 1935 (paper).



## HUMAN BIOLOGY

STUDIES OF DIFFERENTIAL FERTILITY IN SWEDEN.

By Karl A. Edin and Edward P. Hutchinson. P. S. King and Son, London. 78. 6d. 8½ x 5½; 116; 1935.

Dr. Edin's studies on differential fertility in Stockholm have been well known to students of population for a number of years. But it is of the utmost value to have available in English this comprehensive and orderly report on the progress of his work to date. It is the product of a joint effort sponsored by the Institute for Social Sciences of the University of Stockholm and the Social Science Research Council in this country.

The most striking result of the investigation is summarized as follows:

The material analyzed consisted of records for 6,629 Stockholm families. The data were obtained by a combination of the 1920 and 1930 census returns for these families, supplemented by information from the Stockholm birth registers and family registers, and from maternity hospital records.

The classification with respect to economic status was based on the 1920 income of husband, the educational status classification on the husband's degree of education as reported in the 1930 census.

The observed fertility rates increased without exception from the lowest to the highest education groups. The validity of this observation was confirmed by demonstrating:—

1. that the fertility differentials were not produced by a more favorable age distribution or less frequent employment of wives in the more educated groups;
2. that they were not merely the result of the better economic position of the more educated;
3. that they were not a product of temporary changes in fertility during the post-war years;
4. that in all probability they were not a result of social class differences in the number of children born to wives before the observed marriages (illegitimate children plus children of former marriages).



THE MARCH OF MAN. *A Chronological Record of Peoples and Events from Prehistoric Times to the Present Day.*

American Editors: Albert B. Hart and Isaac J. Cox. English Editor: Lawrence H. Dawson. *Encyclopaedia Britannica*, New York, Chicago, London. \$12.00.

11½ x 9; 64 + 96 comparative time charts + 64 plates; 1935.

This superb reference work should be in every library, public or private, home or school, worthy of the name. It is divided into three parts. The first is a historical atlas that includes 96 plates of beautifully engraved and reproduced maps, and some 50 pages of detailed index to these maps. They begin with maps of the world as known to the ancients, and end with the world in 1935.

The second part consists of seven folding "comparative time charts of universal history," backed with linen to stand rough handling. They are printed according to an ingenious color scheme, and altogether constitute the best chronological tables we have ever seen (and we really specialize on chronological tables).

Finally the third, and least important part of the whole is a series of "historical illustrations," good enough in their way, but of no particular interest to the student or scholar.

The aid of a long array of distinguished British scholars was had by those who prepared the volume (George Philip, Ramsay Muir, and Robert McElroy for the Historical Atlas; and Lawrence H. Dawson, the English editor-in-chief, for the Time Charts). These names sufficiently guarantee the soundness of the work.

Altogether we recommend this great work, without reservation, to all and sundry.



THE BANTU TRIBES OF SOUTH AFRICA. *Reproductions of Photographic Studies. Vol. IV, Section I, Plates I-XL. The Vatsonga (The Thonga-Shangaan People). With an Introductory Article on the Vatsonga; a Bibliography, and Descriptive Notes on the Plates, by Henri-Philippe Junod.*

By A. M. Duggan-Cronin. Deighton, Bell and Co., Cambridge. 25 shillings net. 11½ x 8½; 28 + 40 plates; 1935 (paper). Volume IV, Section 1, of this anthropo-



logical study, previous volumes of which have been noticed in *THE QUARTERLY REVIEW OF BIOLOGY*, contains an introductory article by Henri-Philippe Junod on the Thonga-Shangaan, a tribe carefully studied and described by Dr. Henri A. Junod in his valuable monograph *Life of a South African Tribe*. In his brief survey of the present knowledge of Thonga culture he notes how under the different influences the clans have become differentiated and the resulting disintegration of tribal customs and beliefs due to European interference with Thonga life. He says: "No one can underestimate the terrific impact of our civilization on Thonga life; it is overwhelming. Nevertheless . . . the persistence of mystical and spiritual experiences in spite of our matter-of-fact view of life, the steady and growing respect of the educated Thonga for his language and his past, are sufficient proof to me that there are cultural elements in Thonga life which will survive."

There is a bibliography of 8 pages and 40 superb plates showing physical types, manner of dress, architecture, and customs.



*LIFE AMONG THE LAPPS. On the Spring Trek with the Kängämä Lapps.*

By Sven Haglund. Translated from the Swedish by William Savage. Denis Archer, London. 12s. 6d. net. 8½ x 5½; 252, 1935.

This entertaining volume gives the reader an extraordinary clear and wide ranging view of the habits, mode of life, and general philosophy of the nomad Lapps inhabiting the northern reaches of Scandinavia. They are a remarkable people. The Lapps in Sweden number about 7000. They tend over 300,000 reindeer, and get their living from them on land fit for no other use. There is no unemployment among them. As the author says it is probable that they are

tougher and more capable of resisting the weakening influences of civilisation than any other natural race, for it is only the Lapps who have succeeded in performing the difficult task of living the primitive and wandering life of the nomad within the borders of a civilised community. All other races on the same level of civilisation and culture, and living under the

same or similar external conditions, have been poisoned by civilisation, its diseases and its pleasures. They have all perished, mentally and physically. The Lapps alone have been able to withstand the enormous pressure exerted upon them by Nature and civilisation.

The book is abundantly and skillfully illustrated with half-tones from the author's own photographs. It is unfortunate that it lacks any index, because in spite of its chatty narrative style it contains a good deal of useful reference material.



*THE PRIMORDIAL OCEAN. An Introductory Contribution to Social Psychology.*

By W. J. Perry. Methuen and Co., London. 15 shillings net. 8½ x 5½; xi + 380, 1935.

The aim of this book is to study some of the general principles underlying the development of human society in its various phases. The author points out that many peoples, separated by vast distances, and long periods of time, agree in the main concerning the mode of origin of their culture. This suggests that such people look back to a common source of inspiration. The early chapters in the volume are devoted to the most primitive of all peoples—the food gatherers—their fundamental innate tendencies, their behavior in family groups and the development of social institution. The creation stories, so widely held among primitive peoples, concerning the bringing up of land out of the primordial ocean undoubtedly have a definite historical basis. The author discusses at length the fundamental part which this original ocean played in the organization of the early thought of food-producing men. The latter part of the volume deals with the Origins of ideas, the Achievement of excellence and Man and society.

The volume is well documented and contains a detailed index.



*ANTIQUITIES OF THE NEW ENGLAND INDIANS. With Notes on the Ancient Cultures of the Adjacent Territory.*

By Charles C. Willoughby. *Peabody Museum of American Archaeology and Ethnology, Harvard University, Cambridge.* \$4.75. 9½ x 6; vii + 314; 1935.

In this volume is found a detailed account of the archeological discoveries regarding the pre-historic inhabitants of New England. The oldest remains uncovered have been attributed to the pre-Algonquin Indians who probably inhabited the region some 2000-3000 years ago. The implements found include stone-bladed adzes, semilunar knives and bird spears with side prongs. Next in order of time are the artifacts apparently belonging to the Algonquins, close relatives of the Ohio Mound Builders. There are objects of copper, flint arrowheads, perforated amulets, etc. The invasion of the Iroquois separated the Eastern Algonquins from their Ohio relatives, so that the culture of the Algonquins who lived in New England down to prehistoric times differs from that of the original stock and is influenced by contact with the Iroquois. The artifacts ascribed to them include grooved and grooveless axes, mortars and pestles, petroglyphics, pottery, bone implements, copper and metal objects, textile fabrics, etc. Besides full descriptions of the artifacts and of the location of the finds, accompanied by excellent illustrations, the author also presents some reports of early European explorers and settlers.



#### WE SOVIET WOMEN.

By Tatiana Tchernavin. Translated by N. Alexander. E. P. Dutton and Co., New York. \$2.50. 8 x 5½; 304; 1936.

This book is a collection of fifteen sketches of women encountered by the author during her life and wanderings in Soviet Russia. She is now living outside of that country and hence is able to write realistically. She lived through the Russian revolution, afterwards held official posts under the Soviets, and was imprisoned. Her husband suffered deportation to a penal settlement. Under the circumstances it is not strange that she does not like the Soviet system or philosophy. The merit of her book lies in the fact that it recounts only her own first-hand experiences and contacts. The resulting picture

is a dismal one—a picture of ignorance, cruelty, stupidity, filth, official mismanagement, and something nearer to stark savagery than is likely to appeal to sensitive, cultured humanity anywhere. Civilization is a concept notoriously difficult to define precisely. But most people include somewhere in the concept some notions of the decencies and amenities of human living as significant elements. On the basis of a large and growing body of evidence this consideration plays only the smallest of rôles in the Soviet social philosophy.



#### LENGTH OF LIFE. *A Study of the Life Table.*

By Louis I. Dublin and Alfred J. Lotka. Ronald Press Co., New York. \$5.00. 8½ x 5½; xxii + 400; 1936.

This excellent book explains very clearly what a life table is and what it tells its reader about duration of life. Life tables from antiquity to the present are compared and the great improvement in mortality at younger but not at greater ages noted. Life tables for specified causes of death are analyzed, the contributions of medical and sanitary science are discussed, and the conclusion is reached that in the light of present knowledge and without intervention of radical innovations or fantastic evolutionary change in our physiological make-up we may hope to attain a mean duration of life of seventy years. The data on the influence of geographical distribution, heredity, and occupation on longevity are presented, and the application of the life table to population and economic problems is considered. The last chapter gives a detailed explanation of King's and Jenkins' methods of life table construction. An appendix summarizes a large number of life tables for both the United States and foreign countries. This is a book that every person interested in vital statistics or public health should read.



#### KONSTITUTION ODER RASSE?

By Ernst Rittershaus. J. F. Lehmann, Munich. In Germany: 7.40 marks (paper); 8.80 marks (cloth). Outside Ger-

many: 5.55 marks (paper); 6.60 marks (cloth). 9 x 6; 209; 1936.

The object of this book is to examine the relationship between Kretschmer's constitutional types and the somatic habitus supposedly characteristic of different racial groups. After a prolix and ponderous discussion the author concludes that the constitutional type is, in a way, "a more primitive expression of the racial type and an indication of what the racial type will resemble." In other words, an asthenic is such because he belongs to an asthenic race. In his opinion, therefore, Kretschmer's findings on the relationship between habitus and tendency to certain forms of psychosis is not entirely correct because Kretschmer by dividing his material into asthenics and pyknics was actually studying two racial groups whose respective temperament was schizoid and cycloid. In the reviewer's opinion, the only saving feature of this work is the author's sturdy defense of the spiritual qualities of the southern German people. He himself is a southern German. It is noteworthy that in five pages of bibliography each and every publication mentioned is German.



#### BIBLIOGRAPHY OF CRIME AND CRIMINAL JUSTICE, 1927-1931.

Compiled by Dorothy C. Culver. H. W. Wilson Co., New York. \$4.00. 10 x 6½; xl + 413; 1934.

This survey is international in scope and includes material published or in manuscript during 1927 to 1931 inclusive. The system of classification has been based on that used by Kuhlman in his *Guide to Material on Crime and Criminal Justice* but expansion in this field has necessitated many modifications, particularly in the sections on Police. The bibliography is divided into the following sections, each one of which has many subdivisions: Crime and criminal statistics; Offenders; Administration of criminal justice; Police; Criminal law; Criminal procedure; Judicial administration; Punishment; Probation; Institutional treatment; Pardon, parole and indeterminate sentence; and Crime prevention. While the items are entered only once, the detailed subject index

makes it possible for all of them to be easily found. Annotations subjoined to items are informative and descriptive rather than critical. Included in the work is a list of periodical abbreviations and a classification outline. The volume is issued under the auspices of the Bureau of Public Administration of the University of California. It will be of great value to those whose work enters any of the fields listed.



#### POTLATCH AND TOTEM *and the Recollections of an Indian Agent.*

By W. M. Halliday. J. M. Dent and Sons (Canada), Toronto. \$3.75. 8½ x 5½; xvi + 240 + 24 plates; 1935.

The first half of this entertaining volume is devoted to a detailed account of the custom of "potlatch" and its consequences among the Kwawkwalth (stated to be the official spelling of a name more familiar to American anthropologists as Kwakiutl) Indians of British Columbia. The essence of this idiotic institution of potlatch was for a chief to curry popularity by giving away to all and sundry vast quantities of goods, chiefly paid for by the giver with borrowed money. Its whole philosophy, both financial and social, had many other points of similarity to that of the New Deal. Potlatch nearly ruined the tribe fiscally, morally and socially. It is now rigorously prohibited by the Canadian government, with severe penalties for any chieftain who tries to start one. [Reginald, the Office Boy, suggests that we turn Kwakiutl before it is too late.]

The latter half of the book recounts some of the author's experiences during more than twenty-six years as an Indian Agent in British Columbia.

The book contains some valuable material. Unfortunately it lacks an index.



#### ENTRE L'ENCLUME ET LE MARTEAU (1914-1918).

By M. A. Bushins. Paul Dupont, Paris. 15 francs. 7½ x 4½; 343; 1932 (paper).

The author is a Frenchwoman who during the last war lived in the region occupied

by the Germans. In this book she describes her conflicts with the German military authorities: the continuous exchange of insults between her and the invaders; their requisition of material useful for war purposes, foodstuffs, etc., and her attempts to hide what she could. For these activities she was, for a short time, interned in Germany, and this adventure she also relates. In brief, the book is the diary of an emotional woman in whom personal financial losses serve to augment a strong feeling of patriotism, so that every act of the invader is regarded as an insult, injustice, and so on. Even though the avowed purpose of the book is to maintain the feeling of hatred against Germany, still it succeeds in giving a clear glimpse of the economic and social disruption caused by war. The realistic reader will sympathize with the local German officials stationed among hostile people and successfully harried by such an energetic woman.



#### FUNDAMENTALS OF ECONOMIC GEOGRAPHY.

By Nels A. Bengtson and Willem Van Royen. *Prentice-Hall, New York.* \$5.00. 9 x 6; xxviii + 802; 1935.

#### ECONOMIC GEOGRAPHY OF ASIA.

By Daniel R. Bergsma. *Prentice-Hall, New York.* \$5.00. 9 x 6; xxiv + 617; 1935.

Both of these volumes have been prepared as college texts. The first is designed to furnish the subject matter for an introductory course in college geography covering a full course for one-half year, or a year's work on a three hour per week basis. The subject matter is presented in such a way as to develop a scientific and factual background for a better understanding of world production in the realms of agriculture, forestry, mining and manufacturing, and to arouse in the student of social sciences an interest in and appreciation of those influences which are molding present day conditions and activities.

The second volume

is a contribution toward the understanding of the various countries of Asia, their economic-geographic regions, their major commodities, their industries and commerce. It has been the constant aim of the author

properly to evaluate major occupations in the various parts of Asia, and to give a reasoned account of the economic adjustments to the environment rather than the traditional enumeration of facts.

Both of the volumes are abundantly illustrated with figures, graphs, charts and maps, and are well documented and indexed.



#### AFRICA DANCES. *A Book About West African Negroes.*

By Geoffrey Gorer. *Alfred A. Knopf, New York.* \$3.50. 8½ x 5½; xv + 337 + viii + 32 plates; 1935.

This is an uncommonly interesting and informing book of travel in French West Africa, by a young Englishman who is neither a geographer nor an ethnologist in the proper academic sense of having been trained in either of these fields. In spite of this, or just possibly because of it, he manages to tell accurately and entertainingly a lot of the intimate details of negro life and living that everyone wants to know and rarely can find out from more pedantic treatises. Ostensibly his purpose in making the trip was to observe and study native dances. As it turns out the least interesting and significant parts of the book are those devoted to dancing. As Mr. Gorer plaintively says, *writing* about a dance is not much good. The same is true, of course, of music and the graphic arts. But as a document in human biology the book has real and permanent value. The illustrations are neither as numerous nor as good as they might have been. There is an excellent index.



#### THE MANAHOAC TRIBES IN VIRGINIA, 1608. *Smithsonian Miscellaneous Collections, Volume 94, Number 8.*

By David I. Bushnell, Jr. *Smithsonian Institution, Washington.* 50 cents. 9½ x 6½; iv + 56 + 21 plates; 1935 (paper).

The author describes the Indian artifacts found in what constituted Manahoac territory and which extends up the course of the Rappahannock from Fredericksburg

to Kelly's Ford and along the Rapidan from its mouth to Morton's Ford. The objects found include crudely flaked instruments side by side with celts and grooved axes and fragments of pottery with primitive characteristics. No stratified mass of camp refuse was found and so it is difficult to establish the sequence of the occupants of the place. The author arrives at the only possible conclusion, which is that this area has been continuously occupied throughout the centuries but that physical changes such as floods, etc. obscure the order of events. The author also gives a detailed description, including photographs and drawings, of the sites of discovery.



#### HUMAN ECOLOGY.

By J. W. Bews. Oxford University Press, New York. \$5.00. 8 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; xii + 312; 1935.

In the author's opinion the term Human Ecology is the most appropriate to indicate the study of the relationship between man and his environment (physical, chemical, botanic, zoologic, human) and an attempt is made to synthesize what knowledge there is regarding the different forms and effects of these relationships. While the author has ably brought together the findings of many branches of science it cannot be said that his synthesis is very penetrating. What this book really contains are clear summaries of anthropogeography, psychology, anthropology, etc. but not an adequate representation or evaluation of the measure of the interrelations between man and his surroundings. The material has been obtained from standard sources and the bibliography is good.



#### THE FREEDOM OF MAN.

By Arthur H. Compton. Yale University Press, New Haven. \$2.00. 8 x 5 $\frac{1}{2}$ ; xii + 153; 1935.

In this book, based on his Terry Foundation Lectures at Yale University, Professor Compton deals with the bearing of modern

results of physics on the question of human free will. Adopting Lillie's suggestion that our deliberative processes are probably associated with neural reactions on so minute a scale as to have an appreciable uncertainty, he concludes that

such physical laws as the conservation of energy and momentum, the initial conditions and past history, serve to define limits within which action is possible. Within these limits there may be a wide range wherein a man may do as he pleases without violating any physical law. That he actually does as he pleases is a matter of everyday experience. A man's pleasure, in other words consciousness, is thus an additional determining factor which supplements the physical laws in defining his actions.



MELANESIANS AND AUSTRALIANS AND THE PEOPLES OF AMERICA. *Smithsonian Miscellaneous Collections*, Volume 94, Number 11. (Publication 3341.)

By Aleš Hrdlička. Smithsonian Institution, U. S. National Museum, Washington. 25 cents. 9 $\frac{1}{2}$  x 6 $\frac{1}{2}$ ; 58; 1935 (paper).

Doctor Hrdlička traces the history of the theory that Melanese and Australians came to the American continent in pre-Columbian days. This theory is based principally on certain skull measurements which he does not consider as adequate proof. He states that "the dolicho-stenohypsi-cephalic cranium is not extraneous but represents one of the several cranial types of both the Indian and the Eskimo; and that whatever cultural or other resemblances may appear to exist between the pre-Columbian Americas and the South Seas must have other explanations than any material accession of the peoples of the latter parts of the world to the American populations."

There is an extensive bibliography and a table of contents which serves as an index.



JOHN WHITTRIDGE WILLIAMS. *Academic Aspects and Bibliography*.

By J. Morris Stemons. Johns Hopkins Press, Baltimore. \$1.75. 7 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; xii + 109 + 1 plate; 1935.

This interesting biography of John Whitridge Williams, a man much loved and

respected around the Johns Hopkins Hospital, will make many friends among the students, patients and colleagues of the late obstetrician. The book blends within its few pages a pleasing mixture of Doctor Williams' personal traits and professional achievements and leaves the reader feeling he has had the privilege of meeting an interesting personage. A chronologically arranged bibliography of Williams' publications makes a valuable adjunct to the text.



**PRIMITIVISM AND THE IDEA OF PROGRESS in English Popular Literature of the Eighteenth Century.**

By *Lois Whitney*. *The Johns Hopkins Press, Baltimore*. \$2.75. 8½ x 5½; xxi + 343; 1934.

Through most of history the belief has been common that the earliest condition of man was the best, that civilization is a corruption of the natural state of human innocence. With the development of the sciences in the seventeenth century, however, the contrary idea of the general progress of mankind began to spread. In this interesting book Miss Whitney traces the interactions of these two viewpoints, not only in the philosophers of the eighteenth century but in the didactic poets and novelists through whom their ideas reached the general reading public. Professor A. O. Lovejoy contributes a foreword.



**MODERN MAN. His Belief and Behavior.**

By *Harvey Fergusson*. *Alfred A. Knopf, New York*. \$2.75. 8 x 5½; viii + 331 + v; 1936.

The thesis of this interesting book is that in modern civilizations there is not one system of morality but a graded series from rural communities to great cities. In the former the mores cover almost all phases of conduct, while in the latter one enjoys much wider latitude. There is a tendency to a selective adaptation of men to these different social environments: the village-born youth who can benefit by

greater freedom is more likely to migrate to the city than one who feels lost without rigid external standards.



**RASSEFRAGEN IN DER GEBURTSHILFE UND GYNÄKOLOGIE.**

By *G. Frommolt*. *Johann Ambrosius Barth, Leipzig*. 5 marks. 9½ x 6½; v + 96; 1936 (paper).

An interesting approach to the study of racial differences in fertility, age at menarche and physical factors related to child-birth. The author not only brings together in this book pertinent findings in a great mass of literature but also points out leads for further study and stresses caution in differentiating between strictly racial and environmental factors. Some interesting data are added on the incidence of tumors and carcinomas of the uterus and breast among various races.



**ERINNERUNGEN UND WELTEINDRÜCKE EINES NATURFORSCHERS.**

By *Hans Molisch*. *Emil Haim und Co., Vienna*. 9 marks (paper); 10.80 marks (cloth). 8½ x 5½; xii + 232 + plate; 1934.

Molisch, the distinguished plant physiologist of Vienna, was born in Brünn in 1856. The son of a horticulturist, he early became interested in plants. In these pages he tells of his childhood, student days at Vienna and his teachers, his teaching and researches at Graz and Vienna, his colleagues, his two trips around the world and other travels, besides many other interesting things about himself and the persons he has met. The book is illustrated and has an "index of persons."



**WAS IST VOM GEBURTENRÜCKGANG ZU HALTEN? 1, 2.**

By *August Lösch*. *Dr. August Lösch, Heidenheim (Württ.)*. 4.40 marks. 9 x 6; 1, 73; 2, 95; 1932 (paper).

The first edition of this work was the Helfferich prize winner in 1930. In these

two small volumes Löscher attempts to strike a comparative balance of the sum total of economic processes under the influence of different population movements. The problem is treated in an impartial, scientific manner, with the result that the conclusions and the general tone of the whole are not as pessimistic as so many treatises on this subject are apt to be. Singularly enough, the presentation is free from political bias.



#### AUTOBIOGRAPHY.

*By Sigmund Freud. Translated by James Strachey. W. W. Norton and Co., New York. \$2.00. 8 x 5½; 153 + 1 plate; 1935.*

Freud's Autobiography is at one and the same time the story of his life and the history of psychoanalysis. Early in his life he was working on the anesthetic value of cocaine when a chance arose to pay a visit to his fiancée. He left the completion of his experiments to a fellow worker who finally established cocaine as a local anesthetic. Freud himself turned to the study of nervous diseases from which eventually grew his formulation of psychoanalysis. For this new edition he has added a postscript which brings the story of his life up to the present.



**HEALING RITUAL.** *Studies in the Technique and Tradition of the Southern Slavs.*

*By P. Kemp. Faber and Faber, London. (Published in conjunction with The School of Slavonic and East European Studies, University of London.) 21 shillings net. 8½ x 5½; xvi + 335 + 24 plates; 1935.*

Healing Ritual, illustrated with numerous photographs and drawings, is a mass of information collected from the peasants in the outlying parts of the Balkans. Among other things it discusses folk psychology, healing rituals, magic, medicine and doctors, and therapy.

**THE RED SPEARS OF HONAN.** *A Story of Adventure in China.*

*By Escott Lynn. Illustrated by J. R. Burgess. W. and R. Chambers, London and Edinburgh. 3s. 6d. net. 7½ x 5; 320 + 4 plates; 1935.*

A blood-and-thunder tale of revolutionary China, full of bandits, looting soldiers and Bolshevik agents. Needless to say, all the Englishmen and Americans are Galahads while all the Russians are fiends in human form.



#### ZOOLOGY

**INSECT WONDERS OF AUSTRALIA.**

*By Keith C. McKeown. Angus and Robertson, Sydney. 6 shillings. 7½ x 4½; 252 + 16 plates; 1935.*

**BIRD WONDERS OF AUSTRALIA. Second Edition.**

*By Alec H. Chisholm. Angus and Robertson, Sydney. 6 shillings. 7½ x 4½; xiii + 299 + 33 plates; 1935.*

These two additions to a series of books on the natural history of Australia should do much to stimulate popular interest in the subject. The first, by Mr. McKeown, Assistant Entomologist of the Australian Museum, recounts in an entertaining style interesting facts and occasions in the lives of the most remarkable of the Australian insects. The chapter titles alone make an irresistible appeal; for example Child slavery among ants; Ant pastoralists and dairymen; Living honey pots; The carpenter of the grass-trees; Workers in secret—the termites; The ways of crickets; The strangeness of insect courtship. The last chapter on insect foods of the aborigines is of particular interest.

No less remarkable are the Australian birds. In the preface the author says: "The idea behind this book was conceived by the publishers, who considered that Australians, and people in other countries as well, would welcome a gossip account, and one having due respect for accuracy, of the 'Believe-it-or-Not' aspects of Australia's remarkable avifauna." With simplicity and charm he tells of the little Black-capped Honeyeater that steals human hair; of the elusive Heath Wren and its whispered mimicry of other birds' notes; of the Satin Bower-birds and their play-arbours; of the Lyre Bird revels; of

the parasitic Cuckoo that foists its eggs upon other birds; and of the many parrots and other extraordinary and beautiful birds.

Both books are rich in excellent illustrations and each has an index.



**THE LOCUST OUTBREAK IN AFRICA AND WESTERN ASIA IN 1934.**

*By the Committee on Locust Control. Survey prepared by B. P. Uvarov. British Library of Information, 270 Madison Ave., New York. 95 cents. 9½ x 6; 65 + 11 maps; 1935 (paper).*

For the last ten years in Africa and Western Asia there has been an uninterrupted invasion of locusts. The species represented are the Desert, the Tropical Migratory, the Red and the Brown Locust. Four surveys (including the present report) have been made based on monthly reports from the various countries. The first report covered the years 1925 to 1931 inclusive. The others are for 1932, 1933, and 1934 respectively. There has been a continuous improvement in the records sent in. The most serious defect in many of the reports is that the identity of the species of locust concerned is not clearly indicated. Also frequently little or no attention is paid to the collection of records of breeding. Therefore the final surveys deal almost exclusively with the appearance and distribution of the swarms. The question is raised whether when sufficient data have been collected it may not be found that there are no periods, at least in Africa, when swarms of some species of locust are not present. If so, temporary measures could never meet the situation.

The report includes a lengthy bibliography and in a folder inside of the back cover will be found a series of maps showing swarm distributions.



**SNAKE-HUNTERS' HOLIDAY. Tropical Adventures in Search of Bats and the Bushmaster.**

*By Raymond L. Ditmars and William Bridges. D. Appleton-Century Co., New York. \$3.50. 8½ x 5½; ix + 309; 1935.*

Around a lunch table in the New York Zoölogical Park was planned a trip to Trinidad and British Guiana to collect bats and snakes, particularly the bushmaster, of which the Zoo had had no specimen for more than twenty years. A student at the University of Michigan, Arthur M. Greenhall, and a journalist from the *New York Sun*, William Bridges, were sent ahead on a scouting expedition to round up specimens in advance of Dr. Ditmars' arrival. It was Bridges' first collecting trip to the tropics, and he writes entertainingly of the ways of naturalists and the game they seek. In a journalistic style he tells excitingly and amusingly of the search for specimens, the capture of vampire bats in dark, damp caves; expeditions at night looking for frogs and snakes; the unearthing of "the most repulsive creature in the West Indies," the giant centipede; and the fruitless search for the bushmaster. When they returned to Trinidad from British Guiana, however, they found that a bushmaster had been captured by a driller in an oil field and had been turned over to Dr. Ditmars on his arrival. This specimen was brought back to the Zoölogical Park, where it lived for only a little over two months.

Dr. Ditmars writes the first chapter on planning the expedition, and the last chapter on getting the specimens home. The rest of the book is Bridges'. There are excellent photographs and an index.



**STUDIES OF GASTROPODA.**

*By Amadeus W. Grabau. National University of Peking, University Press, Peiping. \$1.50. 9½ x 6½; viii + 159 + 3 plates; 1935 (paper).*

A group of five papers, reprints from various scientific journals. The titles are as follows: Characters of the gastropod shell; *Fulgur* and *Sycotypus*; On orthogenetic variation in Gastropoda; Value of the protoconch and early conch stages in the classification of Gastropoda; The significance of the so-called ornamental characters in the molluscan shell. In the preface the writer calls attention to the fact that little consideration up to the present time has been given to the char-



acters of immature individuals and none whatever to the protoconch. He emphasizes the fact that all the morphological features, including all the so-called shell ornamentations, have a significance which can be interpreted in terms of physiological conditions—that shell modifications are orthogenetic. The author's work is in the direction of determining (for shells of the China coast) standard individuals (morphotypes) wherever perfect material is available for the basis of comparison for each specific group and by working backwards to the Tertiary, to establish, if possible, phylogenetic series. Included in the text are 56 figures and three plates, diagrams, and a table of the genetic relationships of the species of *Fulgur* and *Sycotypus*. There is an index to genera and species.



**AMERICAN BIRD BIOGRAPHIES.** *Containing the Complete Life-Histories of Familiar Birds Written in Autobiographical Form.*

By Arthur A. Allen. With 10 color plates and 10 wash drawings by George M. Sutton. Comstock Publishing Co., Ithaca, N. Y. 9½ x 6½; ix + 238 + 20 plates; 1934.

This set of life histories of twenty of the more familiar of our North American birds makes a departure from the ordinary method of bird descriptions and is written in autobiographical form. Pertinent facts relating to distribution, migration, plumage, and nesting are brought out, but as each story is developed one is made keenly aware of the long and careful observations of the author on the more intimate details of bird life—differences in male and female behavior in nest building and the care of eggs and young, and many little characteristics that would pass unnoticed by the less acute observer. There are many unusual photographs among the 200 with which the book is illustrated. In addition to these photographs taken by Doctor Allen there are twenty full-page water-color portraits made by George Miksch Sutton and ten of these are beautifully done in color.

The book is concluded with a set of

questions for classroom use relating to the life histories of these birds, the answers to which are to be found in the autobiographies.



**INSECT ENEMIES OF SHADE-TREES.**

By Glenn W. Herrick. Comstock Publishing Co., Ithaca, N. Y. \$5.00. 9 x 6; x + 477; 1935.

A book of the utmost importance to all those interested in the preservation of shade trees. The author, professor of economic entomology at Cornell University, through many years devoted to the study of the enemies of trees, is well fitted to write an authoritative treatise on this subject. In the first three chapters are discussed the general methods of protection from insect attack; materials and apparatus for the control of tree and shrub insects, and suggestions for the treatment of weakened trees. Then follow 26 chapters in each of which the insect enemies of an important shade tree are dealt with. The varieties of the insect pests are described, their life histories, the nature of the injuries they inflict, the means of detecting their presence and the best means of control. By a satisfactory method of cross referencing the author has avoided repetition. A final chapter is devoted to miscellaneous insect enemies of trees and shrubs. The 350 drawings and photographs form a valuable part of the book. It is well documented and contains an index of trees and shrubs as well as a general index.



**ETHICS OF EGG-COLLECTING.**

By Eric Parker. The Field Press, London. 5 shillings net. 8½ x 5½; 120 + 1v; 1935. The controversy as to whether the activities of egg-collectors resulted in the diminution of rare British birds began in 1921 when Lord Buxton brought up the subject at a meeting of the Royal Society for the Protection of Birds. In 1934 and 1935 there appeared in the *Field* a series of articles and letters on the subject, and in

this book the editor-in-chief of that journal summarizes the correspondence and clearly shows that at the present time there exists a group of egg-collectors whose activities do great harm to certain rare breeding birds. In the latter half of the book the author discusses various methods of combating the depredations of the insatiable collector "who lifts clutch after clutch from the nests of rare birds, merely for the sake of adding to the numbers of egg-shells in his possession" and considers the question "whether there are any practical steps which can be taken, not merely to enforce the law as regards the protection of rare birds, but also possibly to strengthen it," and comes to the conclusion that the existing provisions of the law are sufficient and merely lack adequate enforcement.



THE FISHES OF NEW ENGLAND. *The Salmon Family. Part 2—The Salmon. Memoir, Vol. 9, No. 1.*

By William C. Kendall. Boston Society of Natural History, Boston. \$4.00 (paper); \$5.00 (cloth). 12 x 9½; 166 + 11 plates; 1935 (paper).

The first part of this memoir on the Salmon Family of New England by Kendall appeared in 1914. The present memoir recognizes and defines the following New England salmonoid families on a basis of their comparative anatomy: Salmonidae, Coregonidae, Argentinidae, and Osmeridae. It deals specifically and in a thoroughly comprehensive manner with the Atlantic salmon (*Salmo salar* Linne), the lake salmon (*Salmo sebago* Girard) and the Presumpscot 'Jumper' (now extinct). Among the chapters are those on habitat, feeding habits, anadromy, life history, history of New England salmon rivers, salmon angling in New England, origin of lake salmon, sizes attained by Atlantic and lake salmon, etc., etc. Considerable historical data are given in tabular form concerning catches and markings and the recapture of marked individuals. A lengthy bibliography is included, also eleven excellent colored plates depicting both Atlantic and lake salmon in various stages of growth.

A CONTRIBUTION TO A BIBLIOGRAPHY OF THE DESCRIBED IMMATURE STAGES OF NORTH AMERICAN COLEOPTERA.

By J. S. Wade. U. S. Department of Agriculture, Washington. Free. 10½ x 8; 113; 1935 (paper).

It is at best a thankless and laborious job to prepare an extended bibliography on any subject. Once done, however, such a compilation has great value to investigators in the particular field covered by the references. Doctor Wade has assembled in the present monograph an excellent series of citations dealing with the immature stages of North American beetles. The material is arranged alphabetically according to genus and species. Each entry, where possible, refers the reader to papers dealing with the following subjects: name of genus; name of species; name of original describer of the imago; notation as to where the first and later descriptions of the immature stages occur, and, information on the "biology" or general economy of the form.

Entomologists will find this a good book to have at hand.



1001 QUESTIONS ANSWERED ABOUT YOUR AQUARIUM. *Toy Fishes—Fresh, Brackish and Salt Water. Also Your Garden Pool and Terrarium.*

By Ida M. Mellen and Robert J. Lanier. Dodd, Mead and Co., New York. \$3.00.

8 x 5½; xiii + 450 + 3 color plates; 1935. Actually this book is misnamed for instead of asking and answering 1001 questions about the aquarium it deals with 1074 and could therefore, with perfect logic, be entitled, "1074 questions answered about your aquarium." The book covers the usual topics; construction and care of the aquarium, tropical fish, gold fish, native fish, the salt-water aquarium, the question of pH, diseases of fish, the outdoor garden pool, and the terrarium. There are a number of drawings and photographs and an unusually good bibliography included in the volume. It is not a book one would care to read from cover to cover since the questionnaire method does not lend itself to such a procedure. However, aided by a com-

plete index the aquarist will find it a useful reference book for his piscatorial problems.



ECOLOGY AND LIFE HISTORY OF THE PORCUPINE (*Erethizon epixanthum*) as Related to the Forests of Arizona and the Southwestern United States. *University of Arizona Bulletin*, Vol. VI, No. 5. *Biological Science Bulletin* No. 3.

By Walter P. Taylor. *University of Arizona, Tucson*. \$1.00. 9 x 6; 177; 1935 (paper).

In the forests of Arizona and other southwestern states the porcupine has been doing considerable damage to the trees. The present study has been stimulated by this fact and data have been gathered on the general ecology of the animal in the hope that the problem of control may be efficiently dealt with. The author places on record many instructive observations on the porcupine's behavior, breeding habits, food habits, enemies, etc., and the book should prove an adjunct to mammalian natural history as well as being useful to the conservationists. Some of the chapter heads, worded in an anthropocentric vein, are rather amusing, e.g., "Has the porcupine any good qualities?" and, "The porcupine an unsocial individualist," etc.



#### CONCERNING THE HABITS OF INSECTS.

By F. Balfour-Browne. *The University Press, Cambridge; The Macmillan Co., New York*. \$1.50. 7½ x 4½; x + 169 + 9 plates; 1935.

This little book, the outcome of a course of lectures "adapted to the juvenile auditory" should be on the shelves of all school libraries. Its object is "not so much to describe the life histories of various insects as to explain how these life histories were worked out, in the hope that others may be encouraged to do similar work." The six chapters are concerned with insect collecting, the habits of bees and wasps, caterpillars, dragon flies, and water beetles, and the

habits of insects and the work of man. Written simply but interestingly the book will be much read by young people and possibly by some who are not so young. It contains a number of plates and figures, a map and an index.

SERPENTS OF THE NORTHEASTERN STATES. *A Guide to the Venomous and Non-venomous Species of the North Atlantic and New England Areas*. New Edition, Revised and Enlarged.

By Raymond L. Dismars. *New York Zoölogical Society, New York*. 50 cents. 9½ x 6½; 40 + 22 plates; 1935 (paper).

This is a simple but complete guide for the identification of the 18 non-venomous and 3 poisonous species of snakes found in the northeastern part of the United States from the Canadian border to Delaware. Following a brief chapter on the identification of snakes, is a key based upon (1) the kind of scales, (2) pattern and coloration, (3) size and (4) shape of the pupil of the eye, "which latter characteristic immediately separates the poisonous species on gross examination"; complete descriptions of the species and general range; brief but adequate sections on precautions against accidents, and the treatment of snake bites. There are 38 excellent reproductions of photographs and one color plate, and a list of eight reference books on serpents.

NOTES ON SOUTH AFRICAN WILD LIFE CONSERVATION PARKS AND RESERVES. *A Report Prepared for the American Committee for International Wild Life Protection*. *Special Publication* No. 7.

By Thomas Barbour and Margaret D. Porter. *American Committee for International Wild Life Protection, Cambridge*. 9½ x 6; 34 + 3 plates; 1935.

At the present time a great effort is being made to preserve particular species of animals and plants rapidly becoming extinct in South Africa, and vast reserves are now being established in Rhodesia, Bechuanaland, Transvaal, Natal, Orange Free State, Basouto, South West Africa

and Cape Province. The authors of this little pamphlet visited South Africa "specifically to gather information and to carry such encouragement as we were able from the American Committee for International Wild Life Protection which has its head office here in the Harvard University Museum." They briefly describe the natural beauties and wild life of these reservations and the efforts that are being made to establish the reserves as permanent national parks. The three plates are excellent.



THE INVERTEBRATA. *A Manual for the Use of Students. Second Edition.*

By L. A. Borradaile and F. A. Potts. With Chapters by L. E. S. Eastham and J. T. Saunders. The Macmillan Co., New York. \$4.00. 8½ x 5½; xv + 725; 1935.

This volume (reviewed in Q. R. B., 7: 483) has been revised primarily by extending the discussion on the structural and functional features exhibited by the metazoa and by adding additional material to the section on the insects. In addition, each chapter has been revised and corrected by its respective author and certain new illustrations have been prepared.

The book, in the opinion of the reviewer the best of the general invertebrate texts, should find new friends in its second edition.



CITIES OF WAX.

By Julie C. Kenly. D. Appleton-Century Co., New York. \$2.50. 8 x 5½; xv + 250; 1935.

"Cities of Wax" may well hold a prominent place among the nature books on the child's library shelf. This is a story of the life of the honey bee told in a moving, dramatic fashion that should immediately gain and hold the attention of the child. It is accurate and instructive and the text is charmingly illustrated with pen and ink sketches. There is an index.

DIE BLATT-MINEN MITTEL- UND NORD-EUROPAS. *Bestimmungs-Tabellen aller von Insekten-Larven der verschiedenen Ordnungen erzeugten Minen. Lieferung 1.*

By Martin Hering. Gustav Feller, Neubrandenburg. Subscription price for 6 numbers: (Germany and Switzerland) 12 marks; (foreign, except Switzerland) 9 marks. 9½ x 6½; ix-xii + 112; 1935 (paper).

This is mainly an identification list, alphabetically arranged by species of plant host, of leaf burrows made by the larval forms of Lepidoptera, Hymenoptera, Coleoptera, and Diptera. The species included are confined to those of central and northern Europe, including England. A work of interest to entomologists and botanists.



DEEP-SEA FISHES OF THE BERMUDA OCEANOGRAPHIC EXPEDITIONS. No. 1—*Family Derichthyidae*. No. 2—*Family Nessorhamphidae*. *Zoologica, Volume XX. Numbers 1 and 2.*

By William Beebe. New York Zoological Society, New York. 50 cents. 9½ x 6½; 51; 1935 (paper).

This paper includes a description of the systematic characters of *Derichthys serpentinus* (Family Derichthyidae) and *Nessorhamphus ingolfianus* (Family Nessorhamphidae) with some interesting remarks on the development and ecological relations of the forms studied.



THE FISHES OF UNION ISLAND, GRENADINES, BRITISH WEST INDIES, WITH THE DESCRIPTION OF A NEW SPECIES OF STAR-GAZER. *Zoologica, Vol. XIX, No. 6.*

By William Beebe and Gloria Hollister. New York Zoological Society, New York. 25 cents. 9½ x 6½; 16; 1935 (paper).

A faunal fish list of Union Island, one of the Grenadines, is presented with notes on each form taken at time of collection. It represents the only published list from this locality.

A BIOLOGICAL RECONNAISSANCE OF NAVAJO MOUNTAIN, UTAH. *University of California Publications in Zoology*, Volume 40, No. 14.

By Seth B. Benson. *University of California Press, Berkeley*. 10½ x 6½; 18; 1935 (paper).

MUTILLIDÆ OF THE PHILIPPINE ISLANDS.

By Clarence E. Mickel. *Minnesota Agricultural Experiment Station, St. Paul*. 10½ x 7½; 129 + 1 plate; 1934 (paper).

THE MUTILLID WASPS OF THE ISLANDS OF THE PACIFIC OCEAN (Hymenoptera; Mutillidae).

By Clarence E. Mickel. *Minnesota Agricultural Experiment Station, St. Paul*. 10½ x 6½; 145; 1935 (paper).

ZOOLOGICA. *Scientific Contributions of the New York Zoological Society, Volume X, Numbers, 2, 3, and 4*. Containing following papers: *Cichlid Fishes in the West Indies with Especial Reference to Haiti, Including the Description of a New Species of Cichlasoma*, by John Tee-Van; *An Annotated List of the Cyprinodont Fishes of Hispaniola, with Descriptions of Two New Species*, by George S. Myers; *Additions to the Fish Fauna of Haiti and Santo Domingo*, by William Beebe and John Tee-Van.

*New York Zoological Society, Zoological Park, New York*. 25 cents. 9½ x 6½; 38; 1935 (paper).

NEVADAN RACES OF THE MICROTUS MONTANUS GROUP OF MEADOW MICE. *University of California Publications in Zoology*, Volume 40, No. 12.

By E. Raymond Hall. *University of California Press, Berkeley*. 10½ x 6½; 11; 1935 (paper).

THE CYCLE OF TRYPANOSOMA CRUZI IN TISSUE CULTURE OF EMBRYONIC HEART MUSCLE. *University of California Publications in Zoology*, Volume 41, No. 3.

By C. A. Kofoed, F. D. Wood, and E. McNeil. *University of California Press, Berkeley*. 10½ x 6½; 2; 1935 (paper).

DIFFERENTIATION IN POCKET GOPHERS OF THE THOMOMYS BOTTAE GROUP IN NORTHERN CALIFORNIA AND SOUTHERN OREGON. *University of California Publications in Zoology*, Volume 40, No. 11.

By Joseph Grinnell. *University of California Press, Berkeley*. 10½ x 6½; 15; 1935 (paper).

A DISTRIBUTIONAL STUDY OF THE PEROMYSCUS SITKENSIS GROUP OF WHITE-FOOTED

MICE. *University of California Publications in Zoology*, Volume 40, No. 13.

By Ian McT. Cowan. *University of California Press, Berkeley*. 10½ x 6½; 10; 1935 (paper).



## BOTANY

POLLEN GRAINS. *Their Structure, Identification and Significance in Science and Medicine*.

By R. P. Wodehouse. *McGraw-Hill Book Co., New York*. \$6.00. 9 x 5½; xv + 574; 1935.

This should be a useful book for botanists and students of hay-fever. It consists of two parts. Part I contains: historical review; methods of collecting and preparing pollen for microscopic examination; atmospheric pollen; hay-fever; pollen grain characters; and a chapter on pollen statistics by G. Erdtman. Part II is a classified list, with descriptions of morphological characters, of fossilized gymnosperms, the pollen grains of most of the wind-pollinated plants, those of the insect-pollinated species which are known or believed to contribute to the production of hay-fever, and allied forms. This is an authoritative work, but the author makes no claims as to its being the final word on the subject. To quote from the preface:

At the present time the discovered is but a small part of the discoverable in pollen morphology. The present work, therefore, cannot be a compendium of much knowledge, if, indeed, such were desirable. Though it presents as far as possible what is known about pollen grains, it does so primarily with the object of bringing out the principles involved in their study, of showing where new discoveries may be made, and of furnishing a reliable method of approach.

The book is significantly illustrated with 14 plates and 123 figures, mostly the work of the author. It is provided with a glossary, a thirteen-page bibliography and an index.



ETHNOBIOLOGICAL STUDIES IN THE AMERICAN SOUTHWEST. 1. *Uncultivated Native Plants Used as Sources of Food*. *The Univer-*

*sity of New Mexico Bulletin, Whole Number 266. Biological Series, Vol. 4, No. 1.*

By Edward F. Castetter. University of New Mexico, Albuquerque. 25 cents. 9 x 6; 62; 1935 (paper).

In a series of bulletins on Southwestern ethnobiology an attempt will be made to bring together "the results of ethnobiological researches which have been done to date in the American Southwest. An effort has been put forth to make the work *comparative*, for it is strongly believed that the ethnobiology of one Indian group compared with similar studies of other groups has a definite, far-reaching value."

While the use of native plants by various Indian tribes of the Southwest has declined since the coming of the Spaniards in 1540, nevertheless many of the groups have preserved to the present day the usage of uncultivated plants as food. The present publication, the first in the projected series, lists alphabetically by scientific name 210 native plants used by some of the Indian groups of the Southwest, particularly the Pueblo Indians of New Mexico, with an interesting discussion of the manner in which the seeds or the plants themselves are prepared for use as food, or for seasoning or coloring foods.

There is a bibliography of 45 titles and a list of the common Indian and Spanish names of the plants referred to in the text.



#### PRINCIPLES AND PRACTICE OF FIELD EXPERIMENTATION.

By J. Wishart and H. G. Sanders. Empire Cotton Growing Corp., London. 3 shillings. 9½ x 6; 100; 1935 (paper).

This study is divided into two parts. Part I deals with the statistical principles and methods of analysis underlying modern field experimentation. The authors have been very conservative in their recommendations of biometric methods and are careful to emphasize that caution must be used in interpretation of statistical results. Much of the statistical applications are based on R. A. Fisher's *Statistical Methods for Research Workers*, and the authors have made the fundamental concepts of that work more comprehensible as they apply to field experimentation.

Part II is concerned with the practical application of the statistical principles discussed in Part I. The authors emphasize the need of repeating experiments and of having adequate controls. Much is said about the suitable size of plots, the arrangement and shape of them and of sampling observations on plots. The survey should be very useful.



#### LABORATORY PLANT PHYSIOLOGY.

By Bernard S. Meyer and Donald B. Anderson. Edwards Bros., Ann Arbor, Mich. \$1.75. 10½ x 8½; vi + 107; 1935.

A first-rate laboratory manual such as this has long been needed by college teachers of plant physiology and the one prepared by Meyer and Anderson is far and away the best one now available. A judicious selection has been made of the standard experiments so that the whole field of chemical plant physiology has been very evenly covered. To these familiar experiments new ones have been added to demonstrate the newer additions to the knowledge of the subject. The descriptions of the procedures for performing the experiments are very well stated. Blank pages are interleaved for the student's notes. Appendices explain several of the laboratory arts in brief, including the use of the analytical balance and the microscope and set forth the formulae for the various reagents required. There is no index but there is a table of contents.



#### PLANT PHYSIOLOGY.

By Meirion Thomas. P. Blakiston's Son and Co., Philadelphia. \$5.00 net. 8 x 5½; xii + 494; 1935.

In the preface the author delineates the book as follows:

The present book has been written to assist students who wish to develop the knowledge of plant physiology that they have acquired in general courses on botany given in the higher forms at school or in the first year at a university. It is therefore hoped that it will prove useful to students of chemistry, physics, agriculture, and other subjects, who have acquired such knowledge, as well as to students who are making a special study of botany.

The text is divided into the following three parts: part I, on the properties of protoplasm; part II, the absorption, translocation and elimination of water, solutes and gases, and, part III, on growth and movement. An appendix contains chapters on biochemistry and physical chemistry.

While this book cannot be considered a complete text on plant physiology, it is, nevertheless, a serious enough work to be of value to students who wish a good survey of the field.



#### ROCK GARDEN PLANTS.

By Clarence Elliott. Longmans, Green and Co., New York. \$3.00. 7½ x 4½; 328 + 16 plates; 1935.

A complete list of Alpine and rock-garden plants is not given in this book, for the author has included only those with which he has had personal experience, and, as a matter of fact, not even all of those for he has frankly omitted those which bored him. However the author is a gardener and collector of wide experience, and persons who are planning to make a rock-garden or have already started one, will find much material in this book to choose from.

On the other hand, this book is more than a catalogue of plants suitable for rock-garden use. To full descriptions of the plants, alphabetically arranged by families, and cultural directions, there are added many interesting reminiscences of the author in collecting species from many parts of the world, and candid remarks about their merits and demerits.

This book should be of interest to the botanist as well as to the English gardener. American gardeners also should find the book of interest, but in following cultural directions will find it necessary to make allowance for differences of climate and temperature. The book is illustrated and indexed.



#### GARDEN VARIETY.

By Sir Arthur F. Hort. Longmans, Green and Co., New York. \$4.20. 8½ x 5½; 255; 1935.

This book essentially comprises four essays: "The Winter of Content"; "A Spring Miscellany"; "Fantastic Summer"; and "Autumn Leaves, which every Wind can Chace." The author was an amateur gardener and collector of plants, well-known in England. One of his chief interests was the collection of as great a number of different plants as limitations of climate and type of soil allowed. In this book he describes his garden and the plants which gave him most satisfaction in the different seasons. Much interesting material on the culture of garden plants and their history is included, but the style seems a little too pedantic for a book of this type. It has been published posthumously by Lady Hort.



#### WOOD HANDBOOK. Basic Information on Wood as a Material of Construction with Data for Its Use in Design and Specification.

By Forest Products Laboratory, Forest Research, Forest Service. U. S. Government Printing Office, Washington. 25 cents. 9½ x 6; 325 + 6 plates; 1935 (paper).

In a practical manner this book discusses: the structure and physical properties of wood; characteristics of the more important commercial woods, their principal localities of growth in the United States, and their specific uses; strength values of various woods; grades and sizes of lumber; methods of preparing wood for various types of construction, gluing, fastening, painting and finishing; wood preservation; fire resistance of wood construction; etc. A glossary, an index, and lists of references at the end of each chapter are provided.



#### THE STORY OF THE PLANT KINGDOM.

By Merle C. Coulter. University of Chicago Press, Chicago. \$2.50. 9 x 6; ix + 270; 1935.

This book was written for liberal arts students who are not necessarily planning to major in science. With a judicious selection of subject matter, the major facts of plant life are presented in a simple and effective way, and the student is given

a well ordered view of the various fields of botany. In tracing the evolution of the plant kingdom Coulter presents both generalized descriptions of the behavior of the members of different orders, and in several cases discussions of the life histories of specific plants—*Marchantia*, for instance. The illustrations are well selected for teaching purposes and there is an unusually complete index.



THE SPECIES OF *TRADESCANTIA* INDIGENOUS TO THE UNITED STATES. *Contributions from the Arnold Arboretum of Harvard University*, IX.

By Edgar Anderson and Robert E. Woodson. *Arnold Arboretum, Jamaica Plain, Mass.; the authors, Missouri Botanical Gardens, St. Louis.* \$2.25. 10 x 7; 132 + 12 plates; 1935 (paper).

This study deals with species of *Tradescantia* found only north of Mexico. The taxonomic history, gross morphology, speciation, hybridization, and taxonomy are discussed at length.



### MORPHOLOGY

REGIONAL ANATOMY. *Adapted to Dissection.*

By J. C. Hayner. *William Wood and Co., Baltimore.* \$6.00. 9 x 6; xii + 687; 1935.

It is distinctly a novel departure to pick up a sizeable anatomy textbook and find that it contains not a single illustration. The author of this book has gone on the assumption that a real need exists for a manual of regional anatomy to supplement the usual systemic texts such as Gray's or Cunningham's. Such a manual will describe the structure of the body in terms of its topography rather than its specific anatomical and functional systems. Doctor Hayner feels that illustrations are not necessary in such a book and has consequently omitted them. Whether laboratory users will agree with him on this point remains to be seen. The book, however, is sure to be of assistance to

the student in the dissecting room and to the surgeon as an aid in visualizing more completely the region of the body to be explored. The text is divided into five sections as follows: one, inferior extremity, abdomen and pelvis; two, upper extremity and thorax; three, head and neck; four, encephalon, and, five, autonomic nervous system. The B. N. A. nomenclature is used.



FASCIÆ OF THE HUMAN BODY AND THEIR RELATIONS TO THE ORGANS THEY ENVELOP.

By Edward Singer. *The Williams and Wilkins Co., Baltimore.* \$3.00. 10½ x 7½; ix + 105; 1935.

This is a rather timely book for it fills the need, which has been growing among anatomists, for precise morphological information about the fasciæ of the human body. The author points this out rather cleverly in his preface when he says,

The dissection methods pay attention to all organs of the body and anatomical atlases bring pictures of them, but the envelopes of these organs, the fasciæ, are mostly left to the imagination of the student. He is able to recognize only a few fascial layers and the fasciæ that he notices are in an artificially changed position giving him an inadequate basis for a proper conception. No wonder that he is inclined to consider the fasciæ as opaque coverings of the organs, which should be speedily removed in order, that he may be able to expose clearly the organs in the short time at his disposal.

This book diagrams and describes with precision and clarity the various fasciæ of the human body and should prove of great value to the anatomist. Since interest is developing in fasciæ from the viewpoint of racial differences the physical anthropologist should also find the volume useful.



AN INTRODUCTION TO HUMAN ANATOMY.

By Clyde Marshall. *W. B. Saunders Co., Philadelphia.* \$2.50. 7½ x 5; 385; 1935.

This is a brief and elementary textbook of human anatomy written "to make the student think of *Anatomy in relation to life.*" The author's interest in writing



the book can be stated in his own words as follows:

... the need became apparent for a simple textbook, written from the standpoint of an anatomist, and containing, in addition to the facts of anatomy in the narrow sense, brief accounts of the functional activities of the different organs, and of related problems of practical interest.

Despite the brevity of the book it is remarkably complete as regards general anatomical features and also has the virtue of being clearly written and well organized. Along with its many illustrations the book should prove useful to those interested in a brief, yet accurate, survey of the structure of the human body.



DEVELOPMENT OF THE PECTORAL LIMB OF *NECTURUS MACULOSUS*. *University of Illinois Bulletin*, Vol. XXXII, No. 52. *Illinois Biological Monographs*, Vol. XIV, No. 1.

By Hsin Kuo Chen. *University of Illinois Press, Urbana*. \$1.00. 10½ x 7; 71; 1935 (paper).

This monograph concerns itself with "(1) the formation of the primordial limb bud and its relations to the myotomes; (2) the differentiation of the limb bud, in which the primordia of the skeleton, musculature, and nerve plexus are laid down; and (3) the further development of the primordia which ultimately attain the conditions similar to that of the adult." The author has emphasized both the experimental embryological and the descriptive anatomical aspects of the pectoral limb and has turned out a memoir that should be useful to comparative anatomists. There are eleven plates following the text and a bibliography.



ANATOMY OF THE RAT. *Transactions of the American Philosophical Society*, Vol. 27.

By Eunice C. Greens. *American Philosophical Society, Philadelphia*. \$5.00. 11½ x 9; xi + 370; 1935.

This excellent anatomical atlas for the albino rat is destined to become a classic. The author has been very thorough and careful in her dissections and in each of the systems she has made careful dissec-

tions of not less than ten rats. The drawings are then based on the conditions existing in the majority of cases. Man has been used as a comparison throughout the work, since it was found necessary to refer to human anatomy texts whenever doubt arose about structures found in the rat.



THE HUMAN FOOT. *Its Evolution, Physiology and Functional Disorders*.

By Dudley J. Morton. *Columbia University Press, New York*. \$3.00. 9 x 6; xiii + 244 + 9 plates; 1935.

This is an interesting and comprehensive presentation of facts about the human foot. The sections on the physiology and functional disorders give evidence to prove that foot trouble is not primarily due to weakness of the muscles and to the existence of an anterior transverse metatarsal arch. The more extensive use of X-ray in diagnosis is advocated. The book is excellently illustrated with photographs and drawings, the latter being particularly informative in the part on evolutionary development. There is a good index and a short bibliography.



THE OBSTETRIC PELVIS.

By Herbert Thoms. *The Williams and Wilkins Co., Baltimore*. \$2.50. 9 x 6; ix + 115; 1935.

The object of this book "is to place before practitioners of obstetrics a working knowledge of those variations and abnormalities of the bony pelvis which may affect obstetric procedure. In addition certain methods of diagnosis as carried out in the clinic with which the author is associated [Yale School of Medicine], are here set in book form for the first time."

Illustrations, an index and a bibliography have been provided.



PRACTICAL COMPARATIVE EMBRYOLOGY.

By A. Richards and A. I. Ortenburger. *John S. Swift Co., St. Louis*. \$1.45. 11 x 8½; 112; 1935 (paper).

This book contains the laboratory directions designed to accompany "An Outline of Comparative Embryology," already reviewed in *THE QUARTERLY REVIEW OF BIOLOGY*, Vol. 7, p. 242.



## PHYSIOLOGY AND PATHOLOGY

A GEOGRAPHY OF DISEASE. *A Preliminary Survey of the Incidence and Distribution of Tropical and Certain Other Diseases.*

By Earl B. McKinley. *The George Washington University Press, Washington.*  
\$5.00. 10 x 6½; xxv + 495; 1935.

This survey, incomplete as it must necessarily be at the present time, will be a valuable aid to investigators and other workers in the field of tropical medicine, besides giving an impetus to the development of this subject both by lay and professional interests. The enthusiastic cooperation which was received in its preparation indicates the recognition of the need and usefulness of such a study. It was made possible by a grant from the American Leprosy Foundation and the Division of Medical Sciences of the National Research Council. The author had as his advisers a committee composed of Doctors F. P. Gay, R. P. Strong, and the late Theobald Smith.

In the introductory chapter is reproduced the form of the entire questionnaire which was employed as a basis for collecting the information which appears in the various tables throughout the book. The division of the survey is as follows: Part I deals with the southern part of the United States and our tropical possessions; Part II, the British Empire; Part III, Asia; Part IV, the Republic of France, the Netherlands and all other countries (26 in number) not covered in the earlier sections. The statistical data are presented in tabular form, the charts or tables being supplemented with various items of factual knowledge regarding the social-economic background of each specific area. No attempt has been made to present an analysis of the data included. In Part V will be found a group of short articles (20 in number) contributed by leading authorities on certain diseases presenting

world problems. Each article is followed by a summary chart which includes all the countries studied in this survey and the number of cases or deaths for each division under consideration. In an appendix is arranged scattered but valuable information from all parts of the world concerning health conditions which it was not possible to include in the main body of the report. The volume is indexed.



THE PATIENT AND THE WEATHER. *Volume I, Part 1. The Footprint of Asclepius.*

By William F. Petersen. *Edwards Bros., Ann Arbor, Mich.* \$3.75. 10½ x 8½; xx + 127; 1935.

This is Volume 1, Part 1, of the series of publications by the author on the relationship between atmospheric conditions and disease. Volumes 2 and 3 have been reviewed in this journal (Vol. 10, pp. 363-4). In this volume the first two chapters summarize the concepts of the Hippocratic school. The following chapters discuss the weather conditions of the United States, cyclonic circulation, barometric variability, etc. On the assumption that atmospheric changes produce significant alteration in the physiologic status of individuals, the author indicates three regions of the United States in which man is subjected to the greatest meteorologic variations. These regions include the New England and Middle Atlantic states, the North Central states and the Pacific states, California apparently excepted. From the statistics on causes of death, defects in drafted men, etc., the author comes to the conclusion that atmospheric conditions in these states are responsible for the comparative decreased fertility and for the higher incidence of heart disease, physical malformations, functional insanities and diseases involving disturbances of the autonomic system. On the other hand, as a group the inhabitants of these states are presumably mentally superior to those of the remaining states. The problem here investigated is very important and deserves careful study, but it must be said that the facts presented by the author

do not demonstrate the validity of his conclusions. The statistical analysis is particularly faulty. The fact that in some states there is a higher incidence of certain diseases than in some other states does not mean that there exists correlation between atmospheric conditions and disease unless it can be shown that, *ceteris paribus*, there is direct association between variation in atmospheric condition and in disease incidence. This the author has failed to do.



THE EFFECTS OF CEREBELLAR LESIONS UPON THE HABITUATION OF POST-ROTATIONAL NYSTAGMUS. *Comparative Psychology Monographs*, Vol. 12, No. 1, Serial No. 56.

By Ward Halstead. Johns Hopkins Press, Baltimore. \$1.75. 10 x 6 $\frac{1}{2}$ ; 130; 1935 (paper).

It has been shown that repeated elicitation causes a decrease in the duration of post-rotational nystagmus. A number of hypotheses have been advanced to explain this "habituation" phenomenon and here the author reports his investigation regarding the effect on pigeons of lesions of the anterior and middle lobes of the cerebellum. Three types of experiments were conducted. The first was to determine whether birds with an experimental cerebellar lesion would habituate as readily as unoperated birds. It was found that at the first trial the post-rotational nystagmus was about equal for both unoperated and operated birds. However, for the latter the habituation effect was markedly and significantly less. The second and third sets of experiments were conducted to ascertain whether a cerebellar lesion influenced birds who had already been habituated. It was found that the operated birds showed a marked loss of the habituation effect while the control group did not. It is noteworthy that a significant degree of habituation persisted in both operated and unoperated birds for as long as three months after the habituation period. The author believes that the habituation effect is of the nature of a "learning process" and therefore from the facts observed concludes that the

cerebellum participates directly in learning situations and may play a dominant part in certain types of "higher" activities. While these ingenious experiments have been well conducted and controlled, it does not seem that this conclusion is warranted without further knowledge regarding the actual mechanism which produces nystagmus and the precise anatomic and physiologic relations between the vestibular apparatus and the cerebrum and cerebellum.



SCENERY AND THE SENSE OF SIGHT.

By Vaughan Cornish. The Macmillan Co., New York; The University Press, Cambridge. \$3.00. 8 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; xii + iii + 10 plates; 1935.

During his travels for many years in England and on the continent the author, from observations of many natural scenic phenomena, came to the conclusion that scenic effects are dependent upon unconscious eye habits. The sun, for example, looks enlarged when it sets because we unconsciously reduce the field of vision. "... the more the eye takes in vertically the more it takes in horizontally and the less impressive are both dimensions. If one may speak of the eye as an organ possessed of personality I should describe this personality as of the kind that can only attend to one theme at a time but has great power of appreciating variations of the theme. By a theme I mean in this connection a visual category, and the categories with which I am dealing ... are height, breadth, distance and area."

There are many other phenomena described and analyzed with a great deal of talk about angles and arcs which at times is only confusing because the author often omits to say just what he is measuring. There are several free hand impressionistic drawings.



THE CEREBROSPINAL FLUID AND ITS RELATION TO THE BLOOD. *A Physiological and Clinical Study*.

By Solomon Katzenelbogen. *Johns Hopkins Press, Baltimore.* \$5.00. 9 x 6; xix + 468; 1935.

This book grew out of an attempt of the author to determine the exact status of our knowledge about the cerebrospinal fluid. Since so much that is contradictory has been published the author felt that it was high time to set down in an organized manner the available data, and to review and analyze it critically.

The book falls into two parts. Part I is chiefly concerned with the origin, mode of formation and circulation of the cerebrospinal fluid. The second part of the book deals with the "physico-chemical constitution of the cerebrospinal fluid, as compared to that of blood in physiological and pathological conditions. In this part the rôle and composition of the cerebrospinal fluid and certain therapeutic procedures are discussed in the light of the present day concept of the function of the barrier between blood and cerebrospinal fluid."

The author is careful to discuss all theories pro and con and in the light of his own research work in physiology and neurology. The book will make an excellent reference source.



SENSATION: ITS MECHANISMS AND DISTURBANCES. *An Investigation of the Most Recent Advances. The Proceedings of the Association, New York, December 27th and 28th, 1934.*

By Association for Research in Nervous and Mental Disease. Editorial Board: Clarence A. Patten, Angus M. Franz, Clarence C. Hare. *Williams and Wilkins Co., Baltimore.* \$7.50. 9 x 6; xxiii + 541; 1935.

This volume reports the Proceedings of the 1934 meeting of the Association for Research in Nervous and Mental Disease. The program of this meeting consisted of a symposium on the neuropathology of sensation. The papers that were presented have been arranged into four sections. In the first are those which discuss peripheral nerves and sensory nerve endings. The second section contains articles on visceral sensations. Articles

concerning sensory tracts and mechanisms in the cord and brain are found in the third part. In the last section are the clinical reports on several forms of sensory disturbances. The majority of articles describe the results of original investigations and in general all contain a fairly complete survey of the literature on the subject.



HOW TO LIVE FOR A HUNDRED YEARS AND AVOID DISEASE.

*A Treatise by Luigi Cornaro, the Sixteenth Century Italian Centenarian. Translated by George Herbert, with an Introduction by George Cooke. The Alden Press, Oxford.* 2s. 6d. net. 7 1/2 x 5; 63; 1935.

Luigi Cornaro lived to be a hundred years old and in his well-known pamphlet attributed his longevity to a restricted diet: a daily ration of 12 ounces of food, consisting of broth, eggs, bread and meat, and 14 ounces of wine. This booklet presents a translation of that pamphlet in addition to an introduction equal to it in length and written by a Mr. George Cooke. This gentleman has a rather low opinion of the diets advocated by medical dietitians and proceeds to say so in a direct fashion. At the same time he demonstrates a rather limited knowledge of the processes of metabolism. It is noteworthy that neither this book nor others of the same kind ever advance one good reason why anyone should want to attain old age at the sacrifice of our one *raison d'être*, satisfaction of physical and spiritual desires.



A TEXTBOOK OF PHYSIOLOGY. *Fifth Edition.*

By William D. Zoethout. C. V. Mosby Co., St. Louis. \$4.00. 9 x 6; 694; 1935.

The fifth edition of this textbook of physiology for dental and pharmacy students has been altered from previous editions (reviewed in Q. R. B., vol. 4, p. 286) by rewriting most of the text and revising and bringing up to date the chapters on hormones, vitamins, muscle physiology and the nervous system.

Many new illustrations, a glossary of commonly used terms, and a list of prefixes and suffixes have been added. Certain supplementary and advanced material has been condensed and set in small type. The book is readable, authoritative, and should continue to be useful for the group it has been serving.



**DIE ORGANISCHEN UND FUNKTIONELLEN ERBKRAKHEITEN DES NERVENSYSTEMS.**

By *Friedrich Curtius. Ferdinand Enke, Stuttgart.* 13 marks (paper); 14.80 marks (cloth). 10 x 6 $\frac{1}{2}$ ; vii + 195; 1935.

The first part of this book, comprising about one-third of the whole, is devoted to a general discussion of the inheritance of diseases of the nervous system and the variability in their manifestation among members of the same family. In the second part each disease is discussed separately with as much information as is at present known concerning the frequency of occurrence, racial and general pathology, anatomy, symptomatology, mode of inheritance, and diagnosis. These diseases are classified as follows by system or type: pyramidal system, spinocerebellar system, extrapyramidal system, diffuse, developmental disturbances, nystagmus and atrophy of the optic nerve, and functional diseases.

Author and subject indices are provided. This is an important book for both students of nervous disease and heredity.



**HEMISPHERIC CEREBRAL DOMINANCE AND HEMISPHERIC EQUIPOTENTIALITY. Comparative Psychology Monographs, Vol. 11, No. 5, Serial No. 55.**

By *Samuel A. Kirk.* Johns Hopkins Press, Baltimore. 75 cents. 10 x 7; 41; 1935 (paper).

Paucity of experimental evidence in support of the opposing theories of hemisphere cerebral dominance and hemisphere equipotentiality in the regulation of certain types of behavior gave rise to

the investigation reported in this monograph. The results indicate that in the case of the rat: (1) hand preference is changed following cortical destruction within a critical area of the anterior portion of the contralateral hemisphere; (2) the hemispheres appear to be equipotential for visual function; and (3) there is no support for the theory of cerebral dominance as applied to intelligent behavior as determined by Maier's reasoning test.



**THE MEDICAL VODOO.**

By *Annie R. Hale.* Gotham House, New York. \$2.50. 8 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; 338; 1935.

This is a frontal attack on vaccination, antitoxins, serum therapy, and the science of immunology generally. It is stylistically more entertaining and more shrewdly put together than the writings of most anti-vaccinationists, but from the viewpoint of logic it is the same old eye-wash. As Augustus de Morgan pointed out long ago the tribe of paradoxers never really changes; they only alter their box of tricks. Mrs. Hale is obviously a sincere person, who honestly believes that vaccination and immunization against diphtheria are nonsense or worse, but so the perpetual motion addict, or the circle squarer, sincerely believes he is right and all the mathematicians are wrong. Nothing can be done about it. But it really does not matter much, because the world and mankind march on regardless of the paradoxers.



**RAPPORT SUR LE PÈLERINAGE AU HEDJAZ de l'Année de l'Hégire 1353 (A.D. 1935).**

*Conseil Sanitaire Maritime et Quarantenaire d'Egypte, Alexandria.* Free. 12 $\frac{1}{2}$  x 9; 113 + 6 plates + folding map and 5 folding tables; 1935 (paper).

This is the report of the health conditions of the Mohammedans who in 1935 made the pilgrimage to Mecca. Compared to 1934, the number of pilgrims this year has increased from 50,000 to 80,000. Thanks to the public health regulations,

which are being enforced with great vigor by the authorities of all countries concerned, such an agglomeration of people has not produced the characteristic epidemics of the past. This report presents data on the number of caravan ships passing the Suez Canal, the number of pilgrims carried, the results of medical and bacteriologic examinations at quarantine ports, the country of origin of these pilgrims and the particular health regulations of each country.



#### CLASSICAL CONTRIBUTIONS TO OBSTETRICS AND GYNECOLOGY.

By Herbert Thoms. Charles C Thomas, Springfield, Ill. \$4.00. 9 x 5½; xxiii + 265 + 1 plate; 1935.

In this book are presented in English fifty-nine selections from the works of eminent contributors and discoverers in obstetric and gynecological practice, from early times up to 1900. The material is grouped under several headings: general obstetrics; the course of labor; the pathology of pregnancy; the operations of obstetrics; puerperal infection; deformities of the pelvis; and gynecology. Brief historical and biographical comments precede most of the selections. Portraits and facsimiles of title pages and text pages of famous works form an interesting feature. The book will be of interest to physicians and students of medical history.



TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. Tome X. *Physiologie Nerveuse*. (Deuxième Partie), Fascicules 1 and 2.

By F. Bremer, R. Causse, A. et B. Chavchard, J. Fromont, R. Garcin, L. Garrelon, J. Huguenaud, A. Hautant, A. Le Grand, F. Lemaître, J.-B. Lorge, L. Merklen, G. Milian, N. Peron, H. Péron, D. Santenaise, A. Strohl, E. Valtier, M. Vidacovich. Published under the direction of G.-H. Roger and Léon Binet. Masson et Cie, Paris. 220 francs (paper); 250 francs (cloth), for two volumes. 9½ x 6½; xv + 1579; 1935.

This is the tenth volume of a series on

human physiology, the previous volumes of which have already been reviewed in this journal. As with the other volumes in this series there are the same defects which arise from the fact that many specialists have contributed to the work. This volume deals principally with the central nervous system. There is an introductory chapter on psycho-physiology, followed by chapters on the physiology of the brain, the cerebrospinal fluid, the cranial nerves, sympathetic and parasympathetic nervous system, the skin, the cutaneous sensory system, languages, auditory, visual, taste and odor.



#### A B C OF THE ENDOCRINES.

By Jennie Gregory. Williams & Wilkins Co., Baltimore. \$3.00. 11½ x 9; xiii + 126; 1935.

This represents an attempt to bring the scientifically determined facts of endocrinology before the layman in a pictorial form that is easily understood. There is no new or original work reported in this book, though there is recent information that has not yet been put in the more elementary books. The book is simple, well thought out, and should help the layman to understand a great deal better all this talk about "glands".



#### QUARTERLY BULLETIN OF THE HEALTH ORGANISATION, LEAGUE OF NATIONS, Vol. 4, No. 3.

World Peace Foundation, Boston and New York. 65 cents. 9½ x 6½; 144; 1935 (paper).



#### BIOCHEMISTRY

HVALRÅDETS SKRIFTER. *Scientific Results of Marine Biological Research*. Nr. 11. *Contributions to the Study of Whale Oils. Chemical Analysis of Samples of Blue Whale Oils*, by I. Tveraaen; *Studies in the Biochemistry of Whale Oils*, by Alf Klom.

Edited by Universitets Biologiska Labora-

*torium*. Jacob Dybwad, Oslo. 10 $\frac{3}{4}$  x 7; 108; 1935 (paper).

The aim of the investigations described in the two papers contained in this publication was "to arrive at a closer understanding of the chemical composition of whale oils, of their formation from the whale's food 'krill' (*Euphasia superba*) in the whale organism, and also to study the laws of the variation to which whale oils are subject."

The samples of oil were collected from various parts of both fat and lean blue whales—about 60 samples from 11 animals—obtained in the Antarctic in 1932–33. The methods of extraction or determination are described, and the chemical content tabulated and discussed. It was found that blue whale oil is of a very complicated composition and contains variable values of iodine and a series of fatty acids. Nine different fatty acids were determined in the prawn oil.

Both papers are equipped with a bibliography.



#### VITAMINS in Theory and Practice.

By Leslie J. Harris. The University Press, Cambridge; The Macmillan Co., New York. \$3.00. 8 x 6; xix + 240 + plate; 1935.

This book is based on four lectures given at the Royal Institution, London, in 1934. The history of vitamin discovery and research is a romantic subject and the author has managed to write a thoroughly readable and enjoyable treatise without departing from actual scientific or historical facts. The vitamins are discussed in the order in which they were first studied: Beri-beri and vitamin B<sub>1</sub>; Pellagra and vitamin B<sub>3</sub>; Scurvy and vitamin C; Vitamin D and rickets; Vitamin A; Vitamin E, diet and sterility. The last chapter is a discussion of what to eat, and as is often the case in such discussions one gathers there is nothing like milk. But there is much sound advice particularly for those families who must be fed on reduced budgets.

#### THE BIOCHEMISTRY OF THE LIPIDS.

By Henry B. Bull. Burgess Publishing Co., Minneapolis. \$3.25. 11 x 8 $\frac{1}{2}$ ; v + 127; 1935.

This monograph on the biochemistry of the lipids is divided into two parts. Part I deals with the chemistry of the fatty acids, soaps, alcohols, hydrocarbons, sterols, fats and oils, phospho-lipids and glyco-lipids. Part II is concerned chiefly with the physiology of the lipids and their rôle in plant and animal life. The intention of the author is to collect and organize all the most recent work on the lipids into a text for students, rather than to report on original research. This monograph should be very useful.



#### INFLUENCE OF LIGHT ON SOME BIOCHEMICAL PROCESSES.

By N. R. Dhar. Society of Biological Chemists, Indian Institute of Science, Habbal P. O., Bangalore. Re. 1. 8 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; 73; 1935 (paper).

An attempt to show that sunlight is beneficial to soil, and plant processes. The author points out from the results of experimentation that both the ammonification and nitrification in soil are remarkably increased by heat and sunlight and that both processes may go on in the presence of sunlight even if there are no bacteria.



TRAITÉ DE CHIMIE ORGANIQUE. Tome III. Hydrocarbures Aliphatiques Saturés et Non Saturés. Longues Chaînes Cycliques. Cyclanes, Cycloènes et Terpènes Monocycliques. Dérivés Halogénés, Nitrosés ou Nitrés des Hydrocarbures Précédents. Industries Dérivées de l'Acétylène. Dérivés Chlorés Industriels.

By J. Doeuvre, G. Dupont, V. Grignard, R. Lespiau, J. Lichtenberger, L. Palfray, L. Ruzicka, F. Swats. Published under the direction of V. Grignard and Paul Baud. Masson et Cie, Paris. 150 francs (paper); 170 francs (cloth); 10 x 6 $\frac{1}{2}$ ; xix + 784; 1935.

The scope of this, the third, volume of a

comprehensive series which will ultimately comprise fifteen volumes, is sufficiently indicated by the subtitles. Volume 1 was noticed in the immediately preceding number of this REVIEW, and volume 2 has not yet been published.



BIOCHEMICAL AND ALLIED RESEARCH IN INDIA IN 1934.

*Society of Biological Chemists, Indian Institute of Science, Bangalore.* Subscription price Rs. 2 per year. 8½ x 5½; 107; 1935 (paper).



SEX

LA CASTRATION CHEZ L'HOMME et les Modifications Morphologiques qu'elle Entraîne. Recherches sur les Adeptes d'une Secte d'Eunuques Mystiques, Les Skoptzy.

By Eugène Pittard. Masson et Cie, Paris.

60 francs. 9½ x 6½; 329; 1934 (paper).

Skoptzy is the name given to a mystic sect found in Russia and Roumania and estimated, in 1871, to number more than 16,000. Its fundamental and distinctive tenet is that "life eternal" can be obtained only by castration. In the males, this is carried out by simply severing the penis and testicles; in the females, by mutilation of the breasts and vagina. Persecution by both the Russian and Roumanian police has not been very effective and it appears that this sect does not lack proselytes. These comprise children obtained in several ways and adults converted either by emotional or economic means.

It is evident that the Skoptzies are an interesting material for study by the physician, anthropologist and human biologist. However they are a suspicious people and very little knowledge about them has been obtained. This contribution by the author is therefore invaluable. He was able to acquire the confidence of some Roumanian Skoptzies and at different periods collected a series of anthropometric measurements on some 50 male adults who presumably had been castrated before puberty (hairless) and on an equal number who had been castrated

after puberty (hairy). The essential findings may be summarized as follows. The hairless Skoptzies are markedly taller than the hairy Skoptzies and the Roumanians in general. In fact, as a group, they are even taller than the Sara negroes. Their superior height is due to an excessive leg length. The head length, breadth and height of the hairless Skoptzies are markedly inferior to those of the other Skoptzies and of the general Roumanian population. This is true also for those indices which present the above head dimensions as percentages of stature. All the other characteristics usually found associated with eunuchism are also observed by the author in the hairless Skoptzies. The hairy Skoptzies, on the average, present no characteristic somatic changes, when compared to the general population, except for some over-development of breasts and buttocks and signs of precocious senility.



SEX IN HUMAN RELATIONSHIPS.

By Magnus Hirschfeld. John Lane, The Bodley Head, London. 8s. 6d. net. 8½ x 5½; xxii + 218; 1935.

Dr. Hirschfeld, recently deceased, was one of the leading investigators in sexology. In this book, of a theoretical and philosophical nature, he summarizes his views on normal and abnormal sexual behavior and illustrates his method of study of the different aspects of the problem. It is interesting to cite his definition of love: "Love is a conflict between reflexes and reflections"; to which he adds: "For every individual, love is determined by the interactions of his psycho-glandular constitution." From this viewpoint the author discusses the interplay between mental attitudes and physiologic reactions in the game called love. The questionnaire submitted to his patients and which he reports has been so prepared as to permit the author to integrate the subject's sex life with his biologic constitution. The book includes chapters on the attraction between similars and dissimilars, fetishism and a critical summary of Freud's theories. Not very well translated, this book appears superficial



and vague in a number of points. However, within its scope, it is satisfactory and the reader will enjoy the author's show of erudition.



#### TOWARDS SEX FREEDOM.

By Irene Clephane. John Lane, The Bodley Head, London. 8s. 6d. net.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; ix + 243; 1935.

An interesting story of the progress of woman during the last hundred years showing the growth in her education and the improvement in her economic position. Beginning with a sketch of Mary Wollstonecraft and her times, the author goes on to describe the place women occupied in the reign of Queen Victoria. She writes of the Contagious Diseases Acts, of child prostitution, of the development of birth control, and of the effect of the World War upon woman by the upheaval of many of the prevailing conventions.



SEX RECOGNITION IN THE GUPPY *LEBISTES RETICULATUS* PETERS. *Zoologica. Scientific Contributions of the New York Zoological Society, Vol. XIX, Number 5.*

By C. M. Breder, Jr., and C. W. Coates. New York Zoological Society, Zoological Park, New York. 20 cents.  $9\frac{1}{2} \times 6\frac{3}{8}$ ; 20; 1935 (paper).

After a series of experiments the authors conclude that sex recognition in the male guppy is feeble and entirely visual, as "any object of appropriate size will stimulate the mating instinct if showing the characteristic motions of a living fish." The female is indifferent to sex activity but fertilization is insured by the aggregating behavior of the species and the great activity of the males. Tables, graphs, and a short bibliography are given.



#### SEX BEHAVIOR IN MARRIAGE.

By Charles A. Clinton. Pioneer Publishing Co., New York. \$2.00.  $7\frac{1}{2} \times 5$ ; 159; 1935.

This book is written for the layman and abounds in sentimentality. It contributes nothing new and is limited in all directions by the moral point of view of the author, who is more interested in asserting that love is a beautiful thing than in discussing it from a technical point of view.



#### BIOMETRY

##### THE GROWTH OF THE SURFACE AREA OF THE HUMAN BODY.

By Edith Boyd. University of Minnesota Press, Minneapolis. \$5.00.  $10 \times 6\frac{1}{8}$ ; xi + 145; 1935.

This monograph is an important contribution to the subject of measurement of the surface area of the body. The author outlines in a thorough and critical manner the different methods of obtaining the values of this dimension either by direct measurements or by estimations. She has abstracted from the literature 231 measurements and attempts to find an adequate mathematical expression of the age variation in the relationships between surface area and weight and height. The results are not satisfactory as the author herself notes. Especially interesting is the graphic representation of the rate of growth of the body surface area. It takes the form of two asymmetrical sigmoid curves. The point of inflection for the first curve is at birth, for the second it is at puberty. To this reviewer it seems that in this case, as well as for a few others, the data permitted a finer biometric analysis. This is the only criticism, if it may be so regarded, of a noteworthy and useful study.



##### ELEMENTS OF STATISTICS. *With Applications to Economic Data.*

By Harold T. Davis and W. F. C. Nelson. The Principia Press, Bloomington, Ind. \$4.00.  $9\frac{1}{2} \times 6\frac{1}{8}$ ; xi + 424; 1935.

As the title implies this excellent textbook was written primarily for the statistical training of students of the social sciences. The relation of statistics to economics is

therefore developed and the problems are drawn from economic sources. Algebraic processes are given in full and the proofs do not presuppose a knowledge of calculus. The appendices give bibliographical notes on early mathematical economists, explanations of logarithms and the use of tables, and tables of logarithms, exponential functions, squares, square roots, reciprocals, ordinates and areas of the probability function, goodness of fit and coefficients for fitting straight lines and parabolas.



#### AN INTRODUCTION TO THE THEORY OF FUNCTIONS OF A COMPLEX VARIABLE.

By E. T. Copson. Oxford University Press New York. \$8.50.  $8\frac{1}{2} \times 6$ ; iv + 443; 1935.

This textbook deals with complex numbers, the convergence of infinite series, functions of a complex variable, Cauchy's theorem, uniform convergence, the calculus of residues, integral functions, conformal representation, the gamma and hypergeometric functions, Legendre and Bessel functions, the elliptic functions of Weierstrass and Jacobi, elliptic modular functions and Picard's theorem. References and exercises are given at the end of each chapter.



#### EINFÜHRUNG IN DIE VARIATIONS- UND ERBLICHKEITS-STATISTIK.

By Erna Weber. J. F. Lehmann, Munich. In Germany: 9.60 marks (paper); 11 marks (cloth). Outside Germany: 7.20 marks (paper); 8.25 marks (cloth).  $8\frac{1}{2} \times 6\frac{1}{2}$ ; 255; 1935.

This book is written for the statistical training of anthropologists, geneticists, and students of constitution. Besides the usual exposition of centering constants, variability, correlation, and probability, methods for determining the applicability of genetic hypotheses from human pedigrees are dealt with. Professor F. Lenz contributes a foreword.

#### MATHEMATICAL TREATMENT OF THE RESULTS OF AGRICULTURAL AND OTHER EXPERIMENTS.

By M. J. van Uven. P. Noordhoff, Groningen. 9.50 florins (paper); 10.50 florins (cloth).  $9\frac{1}{2} \times 6\frac{1}{2}$ ; vi + 309 + folding chart; 1935.

This is essentially a textbook of least squares and analysis of variance. Where the calculus is used in the proofs an alternative proof, involving only elementary mathematics, is also given. A useful feature is a brief glossary of statistical terms in English, Dutch, German, Danish, Swedish, French, Italian, Spanish and Esperanto.



#### CONTINUOUS INVESTIGATION INTO THE MORTALITY OF ASSURED LIVES. Monetary Tables A 1924-29. Vol. I. Vol. II. Vol. III (Joint Lives).

Published on behalf of The Institute of Actuaries and The Faculty of Actuaries in Scotland. University Press, Cambridge; The Macmillan Co., New York. Vol. I, \$22.50; Vol. II, \$17.50; Vol. III, \$11.00.  $9\frac{1}{2} \times 6$ ; Vol. I, xxxix + 339; Vol. II, x + 225; Vol. III, x + 99; 1934-35.

These volumes give mortality functions and monetary tables based on the combined experience of a number of British and a few Canadian and Australian life insurance companies. The original data from which these tables are derived were noticed in Volume 9, page 489, of this Review.



#### PSYCHOLOGY AND BEHAVIOR

##### GHOSTS I HAVE TALKED WITH.

By Henry C. McComas. The Williams & Wilkins Co., Baltimore. \$2.00.  $8 \times 5\frac{1}{2}$ ; viii + 192; 1935.

In 1925 the American Society for Psychical Research decided to employ an experimental psychologist, trained in the methods of the psychological laboratory, to investigate the phenomena in which they were interested. This entertaining book narrates Dr. McComas's experiences in this position. Perhaps the most amus-

ing part of the book is the account of his tests of the celebrated Margery (Mrs. Crandon). Although the conditions imposed by Dr. Crandon made any crucial test impossible, Dr. McComas determined to go ahead with the investigation. However, at the end of one of the séances someone suggested that a thorough examination of Margery and her cabinet be made. "Mrs. Crandon coughed, gagged, leaned over as though suffering from violent *mal de mer*. Then aided by the stenographer she hurried to the bathroom and we could hear a very good imitation of a passenger crossing the English Channel. Dr. Crandon left the room to see his wife. We took a flashlight and examined the floor as we felt that Psyche had been firing blank cartridges. She had."

After this episode Dr. Crandon refused to allow any further investigation. Following nearly a year of fruitless negotiation Dr. McComas arranged a séance of his own in which he reproduced a number of the Margery phenomena, including the ringing of the bell-box, whistling and whispering by the medium using a voice cut-out of the type used by Margery, reading cards in the dark and the appearance of psychic lights. So impressed were the sitters that fifteen of them voluntarily signed a statement that these phenomena were done by no normal means known to them. Five of them, who had been present at Margery's séances, agreed that Dr. McComas's phenomena were quite as good as hers.

Shortly after the séance I wrote to the people who had participated and told them that the Hindoo and I had worked up these effects in order to show Dr. Crandon that what Margery did could be done by natural means and that Dr. Crandon should permit an investigation much more thorough-going than any that he had allowed up to date. Some of my sitters took it all in good part, others were somewhat indignant.



COMPARATIVE PSYCHOLOGY: *A Comprehensive Treatise. Volume I. Principles and Methods.*

By Carl J. Warden, Thomas N. Jenkins, and Lucien H. Warner. The Ronald Press, New York. \$4.50. 8 $\frac{1}{2}$  x 5 $\frac{3}{8}$ ; x + 506; 1935.

This is the first of three volumes under the general title of "Comparative Psychology" and deals with Principles and Methods. The other two volumes will cover Plants and Invertebrates, and Vertebrates.

The aim of the present book is to prepare the student in the background and the fundamentals of methodology so that the later two volumes may be more readily comprehended. The first four chapters give a broad historical and theoretical introduction to the problems of comparative psychology. The next two chapters "Methods of Testing Receptive Capacities" and "Methods of Testing Reactive Capacities" are an attempt to demonstrate in a critical manner the methodology of the science. The final chapter "Comparative Morphology and Physiology of Organisms" deals in a summary fashion with the structure and function of the receptive, transmissive and reactive mechanisms of living organisms.

The work is thoroughly documented and there are nearly a hundred pages of bibliography for the seven chapters. It should be an invaluable reference for the research worker as well as an excellent text.



PRINCIPLES OF ANIMAL PSYCHOLOGY.

By N. R. F. Maier and T. C. Schneirla. McGraw-Hill Book Co., New York. \$4.00.

9 x 5 $\frac{7}{8}$ ; xiii + 529; 1935.

The authors describe in the preface the scope and purpose of their book as follows:

This work is designed to serve as a systematic textbook of animal behavior for courses in psychology and biology. Part I covers the behavior of animals below the mammals, a comparative treatment in which we have endeavored not only to characterize each important animal type but also to work out certain fundamental principles of animal adjustment. In Parts II and III these principles are developed further as the major problems of animal psychology are attacked in connection with the behavior of mammals.

It can be fairly said that the text lives up to the designs held for it by the authors. It should prove a very useful book indeed to the general psychologist. One of the important contributions of the book is that it helps to synthesize and assemble

much experimental work which has hitherto existed only in various isolated papers. Each chapter, as well as the entire volume, is followed by a helpful bibliography.



DÉTERMINISME ET VARIABILITÉ DANS LE COMPORTEMENT DES ORGANISMES. *Actualités Scientifiques et Industrielles*, 261. *Exposés de Biométrie et de Statistique Biologique*, VII.

By W. J. Crozier. Hermann et Cie, Paris. 15 francs. 10 x 6½; 57; 1935 (paper).

In this interesting monograph Professor Crozier shows that when rats run up an inclined plane their mean direction may be fitted with a mathematical function of the angle of inclination of the plane which is capable of a physiological interpretation. The parameters of the function differ from one strain of rats to another, while in crosses they behave as Mendelian characters. The variation is also a function of the intensity of the exciting force. He concludes therefore that the conditions of mechanistic determinism are fulfilled.



ROOTS OF CRIME. *Psychoanalytic Studies*.

By Franz Alexander and William Healy. Alfred A. Knopf, New York. \$3.00. 8 x 5½; viii + 305 + iv; 1935.

A psychoanalytic study of eleven criminal males and females. Beginning with their case histories the authors write fully about each character and carry you through each analysis step by step, often recording in the patients' own words their ideas and dreams, and the analyst's interpretation of them. Most of the analyses were begun in prison and many were continued after the patient's release.



THE FUNCTIONS OF THE VISUAL AREAS OF THE CEREBRAL CORTEX OF THE RAT IN THE LEARNING AND RETENTION OF THE MAZE. II. *Comparative Psychology Monographs*, Vol. 12, No. 2, Serial No. 57.

By Yü-Chüan Tsang. The Johns Hopkins

Press, Baltimore. 75 cents. 10 x 6½; 41; 1936 (paper).

The first part of this study was reviewed in THE QUARTERLY REVIEW OF BIOLOGY, Volume 10, p. 373. This paper is a report of further investigations along the same line. The experiments indicate that there is a non-visual function of the visual cortex, although its exact nature has not yet been determined.



## DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

OUTPOSTS OF SCIENCE. *Journey to the Workshops of Our Leading Men of Research*.

By Bernard Jaffe. Simon and Schuster, New York. \$3.75. 9½ x 6; xxvi + 547; 1935.

The writing of a first rate book on semi-popularized science is a difficult task. To do a good job the author must combine accuracy of statement without sacrifice of interesting reading. Consequently, many such books fail to meet the standards set by the experts, the reading public or both. The present volume should prove an exception however, for it is, by and large, both interesting and authoritative. Doctor Jaffe has selected his topics and personalities with care and has developed his thoughts and opinions realistically and with a minimum of exaggeration.

The book is divided into two parts: part I, dealing with the biological topics and part II, with physical topics. In the biology section the author stresses the work of Morgan in genetics, Hrdlička in anthropology, Welch in pathology, Slye in cancer, Abel in endocrinology and pharmacology, Meyer in psychobiology, McCollum in nutrition, and Howard in entomology. Each of these discussions attempts to point out the major principles of the several fields and to evaluate the contributions of the various personalities in their respective niches. The reviewer found all of the chapters interesting and had no quarrel with the approach except in the chapter on entomology where Doctor Jaffe spends the entire time discussing the economic field of insect control and eradication. Interesting and important

as this subject is it seems a pity that more data on the theoretical entomology were not included.

On the whole, this is an excellent volume and should be read and enjoyed by professional and lay persons alike. Page-sized portraits of most of the scientists discussed make an interesting addition to the text.



#### ARISTOTLE'S CRITICISM OF PRESOCRATIC PHILOSOPHY.

By Harold Cherniss. *The Johns Hopkins Press, Baltimore.* \$4.00. 9 x 5½; xvi + 418; 1935.

A sound, thorough, and scholarly treatise, of great value to serious students of the history of science. Its purpose is in general to examine objectively, and apart from what later commentators said about them, the views of Aristotle's predecessors. This is done with great thoroughness, meticulous documentation, and penetrating scholarship. The author justifiably hopes that the investigation should lead to a better comprehension of Aristotle's own philosophical method,

for once the reports and critiques have been returned to their proper contexts and their relationship to those contexts analyzed, Aristotle's own conception of the unity of his work both in itself and as the culmination of all previous thought assumes a new significance. In the light of this relationship, too, it may appear that the proper approach to Aristotle's systematic philosophy is that which corresponds with his own notion of the origin of his system, namely by way of his predecessors both in their true historical form and in their metamorphosis as lipping Aristotelians.



#### THE ATTITUDE OF VOLTAIRE TO MAGIC AND THE SCIENCES.

By Margaret S. Libby. *Columbia University Press, New York.* \$3.75. 8½ x 6; 209; 1935.

It was inevitable that a man with the intellectual curiosity of Voltaire, living in an age of great scientific progress, should take a lively interest in the sciences. His *Elements of the Philosophy of Newton* con-

tributed much to the spread in France of knowledge of the Newtonian system. Nor was Voltaire content with the rôle of popularizer of science. He busied himself with experiments in physics, on which he based an *Essay on Fire* which he hoped would win him admission to the Academy of Sciences. In biology he held to the old idea of the fixity of species and ridiculed such early evolutionists as de Maillet, while his best remembered contribution to geology is the flippant suggestion that the fossil shells found in the Alps had been dropped there by pilgrims. The book contains a bibliography of 22 pages and an index.



#### MAN THE UNIVERSE-BUILDER. *Backgrounds and Foundations of the Scientific Technique. First Revised Edition.*

By Richard E. Lee. *The Williams & Wilkins Co., Baltimore.* \$3.00. 8½ x 5½; xix + 443; 1935.

In this textbook for an orientation course in the sciences their history and fundamental methodology are described as well as an account of the fundamental concepts on which present-day science is based. Particular attention is given to the development of the concept that energy in its two essential aspects of electricity and radiation is the fundamental stuff of the universe. The concept of evolution is also traced in both its cosmological and its biological applications. Suggestions for further reading and an index are given.



#### AN OPEN LETTER TO COLLEGE TEACHERS.

By Fernandus Payne and Evelyn W. Spieth. *Principia Press, Bloomington, Ind.* \$3.25. 8½ x 6; xiii + 380; 1935.

This book discusses and criticizes teaching in American colleges and universities today. The need for improvement is realized and changes are suggested. There is very little that is new, the material could have been more compactly organized, and the style is verbose. An extensive bibliography and a good index are included.

THE NEXT HUNDRED YEARS. *The Unfinished Business of Science.*

By C. C. Furnas. Williams & Wilkins Co., Baltimore. \$3.00. 8½ x 5½; xiv + 434; 1936.

The Next Hundred Years, entertainingly written in the language of the layman, points out what the scientist has yet to accomplish and shows the deficiencies in science up to date. The book is divided into five parts: Biology, Chemistry, Physics, Engineering; and the whole discussion generally summed up in the final section, Social Consequences.



CAMBRIDGE READINGS IN THE LITERATURE OF SCIENCE. *Being Extracts from the Writings of Men of Science to Illustrate the Development of Scientific Thought.*

By William C. D. Dampier-Whetham and Margaret D. Whetham. The University

Press, Cambridge; The Macmillan Co., New York. \$1.00. 7½ x 5½; xi + 275 + 8 plates; 1935.

The extracts in this book have been chosen to illustrate the development in the thought of succeeding ages of cosmogony from Genesis to Eddington, of the atomic theory from Lucretius to Rutherford, and of the theory of evolution from Aristotle to Bergson.



FRENCH SCIENCE and Its Principal Discoveries Since the Seventeenth Century.

By Maurice Caullery. French Institute in the United States, New York. \$1.25. 7½ x 5; xi + 229; no date.

A review of this book in the original French will be found in THE QUARTERLY REVIEW, Vol. 9, page 258. This translation by the author is good except for the occasional retention of French word order and idioms.





# THE QUARTERLY REVIEW of BIOLOGY



## CHARACTERS COMMON TO HIGHER PRIMATES AND CHARACTERS SPECIFIC FOR MAN

By ADOLPH H. SCHULTZ

*Laboratory of Physical Anthropology, Johns Hopkins University*

(Enlarged revision of address given by the author as retiring president of the American Association of Physical Anthropologists at its meeting in New York City, May 8, 1934.)

### INTRODUCTION

THE scientific investigation of anthropoid apes had its inception at the close of the seventeenth century, when Tyson (1699) published his anatomical description of the chimpanzee. All the early students of the "man-like apes" were greatly impressed with the similarity to man of the great apes. Their writings and, particularly, their illustrations emphasize and frequently exaggerate the *human* qualities of the *apes*. Beginning with Darwin, Huxley and Haeckel this emphasis became reversed so that most modern comparative investigations concern themselves with the *ape-like* qualities of *man*. This last and extremely productive period of research on higher primates has somewhat neglected the at least occasionally needed emphasis on the *specifically human* characters of *man*.

The enormous mass of recent work on the degrees of resemblance between different types of primates has brought about a

very encouraging and almost universal unanimity of opinion in regard to the problem of the particular group of primates to which man must be assigned. When critically weighed, all pertinent facts at our disposal force us to the conclusion that man's taxonomic place is in the second suborder of primates (*Anthropoidea* or *Simiae*) and here in the second series, the *Catarrhinae*. Again there is no room for doubting that man shows much less resemblance to the first catarrhine family (*Cercopithecidae* or *Lasiopygidae*) than to the remaining families, the *Hylobatidae* and the *Pongidae* which, together with man, constitute the so-called higher primates. It is in regard to the more detailed and most ambitious problem of man's exact relationship to the other higher primates that the many students of this subject have as yet not reached a general agreement. Keith (1934) has recently shown that man's family tree can to-day be constructed with mostly unhesitating and little disputed



lines up to the common ancestor of all higher primates, but the places of branching of the terminal twigs leading to recent man and anthropoid apes have been subject to widely differing interpretations. A somewhat extreme view has been taken by Osborn (1927) who states: "... the better we understand the human anatomy and mechanism of both the hand and foot and the more we learn of the fossil ancestors of man, the less close appears our relationship to the great anthropoid apes. . . ." A figure entitled "Osborn's present theory of the ascent and phylogeny of man" published by Osborn in 1930 shows the ancestral stem of the family tree of higher primates dividing at one and the same level (Oligocene) into the human branch on one side, the gibbon branch on the opposite side, and a common branch for all great apes in the middle. Sharply contrasting with this view is the interpretation of Smith (1924), as represented by a family tree in which the gibbon branch is the first to separate from the line leading ultimately to man, the former being followed by a branch for the orang-utan, then by one for the chimpanzee and, last of all, by one for the gorilla, which diverges from the human branch in the second half of the Miocene period. This claim of the closest kinship of man with the gorilla is also expressed in the following statement by the same author: "Any one who is familiar with the anatomy of Man and the Apes must admit that no hypothesis other than that of close kinship affords a reasonable or credible explanation of the extraordinarily exact identity of structure that obtains in most parts of the bodies of Man and Gorilla." Practically the same pedigree as that by Smith has been adopted by Broom (1930). Based upon his comprehensive survey of anatomical similarities between man and other primates Schwalbe (1923) has expressed the conclusion that

man and chimpanzee are not only most alike but were the last to separate phylogenetically and this perhaps not before the beginning of the Pliocene period. The most extreme view in this direction has been reached by Weinert (1932) whose primate family tree shows the chimpanzee as the last anthropoid ape to branch off the line leading to man and this not until the *end* of the Pliocene! These and some of the intermediary interpretations of the phylogenetic relationships between the recent higher primates are shown in Figure 1. Many additional, more or less differing pedigrees have been published, of which only two of the more recent ones may here be mentioned: Based upon his studies on fossil material, Abel (1934) concludes that there exists a sharp demarcation between the phylogenetic lines for chimpanzee, gorilla and man on one side and those for the remaining higher primates, the orang-utan and gibbons, on the other side. In the family tree, proposed by Abel, the African apes and the *Hominidae* are shown to branch from a common ancestral group, the genus *Dryopithecus*. The line leading to the latter separates from the line leading ultimately to orang-utan in the middle Oligocene, and the *Hylobatidae* diverge from the stem of all higher primates in the Eocene period. In striking contrast to this view stand the conclusions by Werth (1921-1928) which are also largely based upon palaeontological evidence. According to this author a common ancestral primate of the Oligocene gave rise to the three great apes on one side and to the early progenitor of the gibbons and man on the other side. Several authors, notably Pilgrim (1915), had previously favored the view that the gibbons stand particularly near the line of human ascent. With the exception of the last example, all these pedigrees by different authors are alike in

regard to the general grouping of the recent higher primates. If man is placed on the extreme left, the two recent African apes are the nearest to man on the right (the gorilla nearer than the chimpanzee according to Smith, 1924, Sonntag, 1924, Morton, 1927, Osborn, 1930, Schultz, 1930a, Broom, 1930, Keith, 1931, and Clark, 1934; and the chimpanzee nearer than the gorilla according to Schwalbe, 1923, Gregory, 1927, Weinert, 1932, Mollison, 1933, and Abel, 1934). The

ences of opinion. Direct fossil evidence, though of invaluable assistance, is unfortunately as yet far too fragmentary to solve these detailed questions in a decisive manner. The at first so promising serum-precipitin tests of the blood have recently been found to be of very limited value in tracing phylogenetic relationships (Zuckerman and Sudermann, 1935, and others).

By comparing the pedigrees in Figure 1 it is seen that the most striking discrepancy among them consists in differences

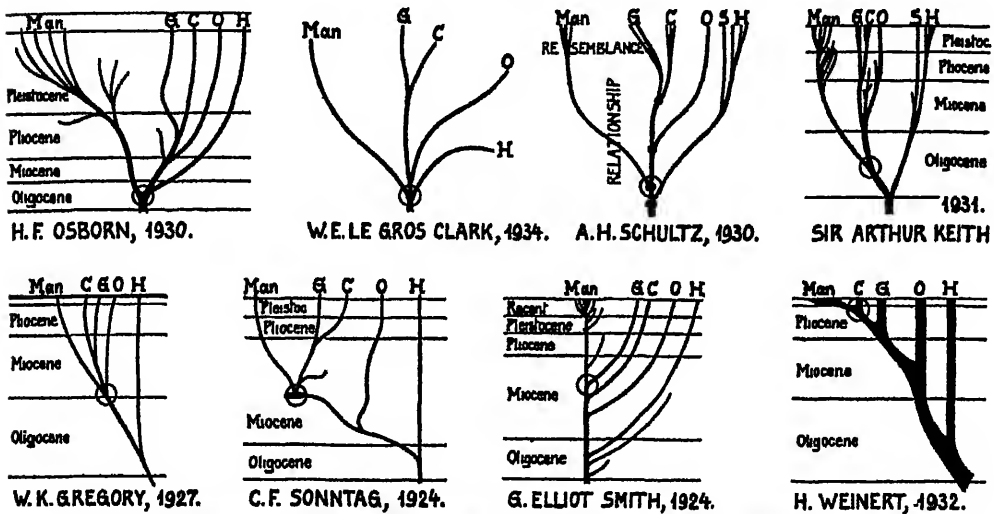


FIG. 1. THE FAMILY TREE OF THE HIGHER PRIMATES ACCORDING TO DIFFERENT AUTHORS

The circles have been added to indicate the place of the last common ancestor of man and any other primate. To facilitate comparisons some of the pedigrees were reversed so that Man appears in all figures on the left side. G = Gorilla; C = Chimpanzee; O = Orang-utan; S = Siamang; H = Gibbon (or *Hylodactylus* in general).

African apes are invariably followed by the orang-utan and the gibbons are found without exception on the extreme right of the pedigrees. This quite generally agreed upon arrangement of the terminal twigs of the family tree is based on the approximate, average degrees of resemblance between the different forms of higher primates. Where some of these recent twigs arise from the older branches and how the latter grow from the common original stem, are the problems in regard to which there still exist marked differ-

ences in the relative position of the exact place of separation of an independent phylogenetic line for man. The places of divergence in the evolutionary courses of the other higher primates differ in the various pedigrees chiefly in regard to geological periods, whereas comparatively little in regard to the order of their occurrence. The most essential problem, therefore, is considerably narrowed, namely to the question whether a separate phylogenetic branch for man started before, at the same time as, or after the

branches for the recent great apes began to diverge. The answer to this question must rest largely upon a comprehensive and unbiased survey of the *relative* degrees of resemblance between all the different higher primates. If the aggregate resemblance between man and any other recent higher primate is closer than that between any two of the apes, it must be assumed that the former two are taxonomically and genetically more closely related than the latter two and that hence the former had a less remote common ancestry than the latter. If, on the other hand, man and even gorilla or chimpanzee resemble one another less closely than the African apes resemble the Asiatic ones, we are forced to conclude that in all probability man branched from other higher primates before any differentiation had taken place into lines leading to the recent great apes. Any attempted determination of the place of phylogenetic separation of the family *Hominidae* must deal also with the following pertinent questions: Does man possess any peculiarities not to be found in the apes, but connecting the former more closely with the lower catarrhines? Have some of the many evolutionary trends, common to all higher primates, progressed to a lesser degree in man than in the anthropoid apes?

By merely comparing the degrees of resemblance between the various higher primates it is frequently impossible to decide whether some peculiarity of a particular primate represents the retention of a primitive, original condition or a high specialization due to unusually rapid evolutionary change. It is necessary, therefore, to compare the characters studied with the same characters in lower primates. From comparisons between the degrees of similarity of different primates in regard to features which vary indi-

vidually to a considerable extent no conclusions can be drawn until large series of specimens have been investigated, which supply the chances for finding those sporadic variations which are frequently of decisive significance in the reconstruction of the ancestral genetic endowment of an animal. The discovery of rare individual variations can at times also change the phylogenetic interpretation of features supposedly restricted to only one type of primate. For instance, the *peroneus tertius* muscle, once regarded as peculiar to man (being present in about 91 per cent of whites), has later been found in a number of gorillas, in a chimpanzee and, most recently, even in a baboon (Wells, 1935). A homologous structure has also been described in a marmoset (for further details see Straus, 1930). It is not the muscle itself, therefore, but only the high frequency of its occurrence which is typical for man.

In speaking of the pervasive likeness of the skeletons of chimpanzee, gorilla and man, Gregory (1934) has recently stated: "the resemblances are largely qualitative, the differences are for the most part quantitative." The same can be said of a great many other bodily structures, indeed, one may even claim that the large majority of the characters common to all higher primates are in a restricted sense of a qualitative nature, whereas the characters specific for man or for any other higher primate are in most instances quantitative. Since the quantitative differences between the various higher primates have so far been much less intensively studied than the qualitative similarities and since the former are specially suited for establishing the much needed *relative* degrees of resemblance, this paper will deal predominantly with quantitative characters. Quantitative and, especially, metric methods of investigation are of great help in

taxonomic and phylogenetic problems by, first of all, replacing general impressions, recorded in words alone, by precise measurements, expressed in impersonal figures which can readily be compared with one another. Furthermore, these methods, when skillfully applied, enable the observer to find significant quantitative differences where hitherto we have frequently been content to speak of qualitative likenesses only. For instance, ischial callosities or frontal sinuses are not merely "qualitative" characters of certain primates, but are really structures differing among some primates quantitatively in regard to frequency of occurrence, age of appearance and relative size. The lack of an outer tail represents a qualitative likeness of all higher primates which supports the assumption that they form one natural group, but permits no further conclusions in regard to the more detailed problems of the genetic subdivisions within this group. Help for the latter problems is gained only through the quantitative study of the degrees of reduction in coccygeal vertebrae and muscles. By the quantitative methods of physical anthropology, particularly by investigations of the body proportions, it is possible to demonstrate that all higher primates are qualitatively alike in sharing the same evolutionary trends, such as widening of the shoulders, hips and chest and lengthening of the arms and of the neck, and that they are quantitatively different by having been carried to widely differing levels along the same trends (Schultz, 1933b). It seems quite evident that detailed, quantitative differences can and must change phylogenetically before the more general, qualitative similarities become noticeably altered. In other words, quantitative characters, such as relative size or frequency of a structure, can in most instances change more easily and rapidly during evolution than the apparently more

tenacious qualitative features, such as categoric presence or absence of a structure. Many basic qualitative changes are merely the result of preceding and gradual quantitative changes.

The following notes, based largely upon the author's own studies, naturally can not claim to give a final answer to this fascinating question of man's genetic relationship to his nearest simian kin, but are intended merely as a contribution toward the eventual and systematic solution of the problem which will have to rest upon all available information as well as upon many additional data yet to be gathered.

Finally, it should be emphasized again that by dwelling upon the differences between man and other higher primates, the author does in no way contradict or even wish to weaken the widely accepted conclusions that man and the anthropoid apes are more closely related than man and any other primates and that man *resembles* in general most closely the gorilla and chimpanzee. Indeed, it is precisely on account of his firm and repeatedly stated (Schultz, 1927, 1930a, 1931, 1933b) conviction of the unassailable finality of these broad conclusions that the author considers it timely and necessary to turn to the logically following and more detailed problems of man's specific characters and their phylogenetic implications for the determination of man's exact place on the family tree of the comparatively few higher primates.

#### SIMILARITIES AND DISSIMILARITIES BETWEEN MAN AND ANTHROPOID APES

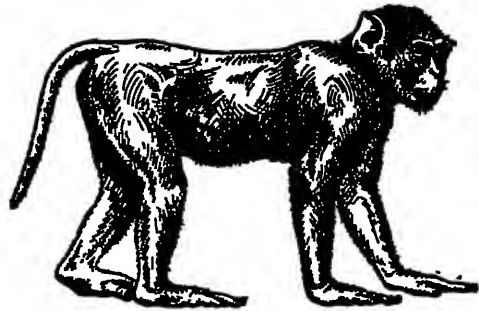
##### *Human Infants*

One of the most persistently quoted and also one of the least justifiable examples of anthropoid ape heritage in man goes back to the well known picture by Robinson, published by Romanes (1892), of a human

infant hanging by its arms and thus "supporting its own weight for over two minutes" and the accompanying statement that this surprisingly great grasping power of the human newborn "refers us to our quadrumanous ancestry — the young of anthropoid apes being endowed with similar powers of grasping, in order to hold on to the hair of the mother. . . ." This temporary grasping reflex in man can not be regarded as indicative of a special anthropoid ape phase in human evolution because, as shown by Richter (1931), the same reflex is much more strongly developed in infantile macaques, which (though no "brachiators") can hang with one hand alone for over thirty minutes. At the age of 2½ months the healthy chimpanzee "Peter" of the Yale Laboratories of Primate Biology could hang by both hands for only one minute (according to the author's examination made with the kind permission of Prof. R. M. Yerkes). This grasping power is of much greater ontogenetic than phylogenetic interest.

There exists, however, another feature, connected with the hands of human infants, which does seem to be of some help in phylogenetic conclusions since it differs radically in different groups of primates. Hrdlička (1928, 1931) has shown abundantly that many human infants walk or run spontaneously on all fours and this invariably with the palms flat on the ground and the fingers completely extended. As shown by Figure 2, this horizontal position of the hands in man is identical with the position of the hands in macaques walking on the ground, but differs very significantly from the upright position of the hands with flexed terminal and middle phalanges in the chimpanzee on all fours. As is well known, the gorilla and the orang-utan also support their weight in quadrupedal

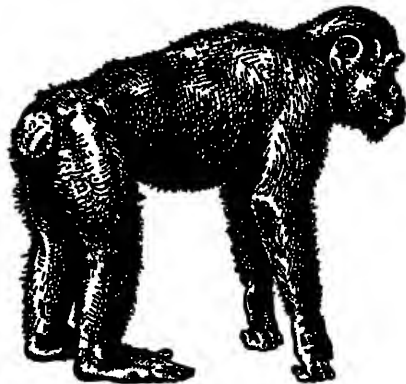
position on the knuckles of the flexed fingers and not, as all arboreal lower



MACAQUE



HUMAN INFANT



A.H.S.

CHIMPANZEE

FIG. 2. SIDE VIEWS OF ADULT MACAQUE, HUMAN INFANT (after Hrdlička, 1928, Fig. 9), AND ADULT CHIMPANZEE IN QUADRUPEDAL POSTURE, SHOWING POSITION OF HANDS IN WALKING

catarrhines and infantile man, on the wrists with extremely extended phalangeal

and metacarpal portions of the hands. Weidenreich (1931) has already pointed out that in the largely terrestrial baboons and red guenons the body weight is usually supported on the metacarpo-phalangeal joints II to V with the metacarpus held perpendicularly, but with the fingers hyperextended and directed forward, as in all other monkeys, and not backward, as in the great apes. In walking infantile monkeys and apes the hands are already held like in the adults, as is shown, for instance, in the excellent photographs of a baby macaque by Foley (1934), of an infant chimpanzee by Jacobsen, Jacobsen and Yoshioka (1932), and of an infantile gorilla by Reichenow (1921). A photograph of "a baby gibbon learning to walk" (kindly supplied by Miss B. White) shows the animal walking in quadrupedal fashion (a mode of locomotion not practiced by adult gibbons) with the palm on the ground, the hand *extended*, and the fingers *completely straight*.

That the great apes do not place their hands on the ground in the manner of man, gibbons, and macaques is not a mere habit, but an anatomical necessity. This had already been carefully stated by Wilder (1862) who, in dissecting a chimpanzee, had found that: "The tendons of the deep common flexor of the fingers were so short as not to permit the simultaneous extension of both hand and fingers; . . . It also readily accounts for the Anthropoids not being able to apply their palms to the ground when on all fours, but being obliged to rest on the knuckles." On the fresh bodies of macaques and of human beings the hands with completely straightened fingers can easily be extended until they form nearly or fully a right angle with the forearm. On the fresh body of a chimpanzee, however, the fingers become automatically flexed, and this with great force, when one

attempts to extend the metacarpal portion of the hand even to only a very slight degree. In a very careful study Virchow (1929) has shown that in the orang-utan the hand (with strongly flexed fingers) can still be extended to as much as 90°, but that in the chimpanzee not even the metacarpal part of the hand can be extended appreciably. Such extension, without releasing the flexure in the fingers, does not become possible until the *palmaris longus*, *flexor carpi radialis* and *flexor carpi ulnaris* have been cut, and even then marked extension is still prevented by a volar ligament between *lunatum* and *capitatum*, a ligament which does not exist in man according to Virchow.

In regard to the attitude of the hands, particularly the fingers, in quadrupedal locomotion and in regard to the anatomical ability to extend the fingers together with the hand man differs radically from the great apes and resembles the gibbons and lower catarrhines.

#### *Ischial Callosities*

Even in very recent books on primates (e.g., Weber, 1928; Maurer, 1928; Jones, 1929; Clark, 1934) it is still claimed that ischial callosities occur among the higher primates only in the *Hylobatidae* and that their complete absence in the great apes and man constitutes a primitive condition since "there is no evidence that they have ever passed through an evolutionary stage in which callosities were developed" (Clark, 1934). In 1927 the writer had already collected some of the scattered data by other authors, which show that ischial callosities do exist sporadically among the great apes and he had demonstrated then, and by means of additional material in 1933 (a), that these callosities develop relatively much later in ontogeny in gibbons and siamangs than in the lower catarrhines. In the following notes the

old and new evidence for the occurrence of ischial callosities in the great apes will be briefly reviewed in order to show that we can actually witness the gradual evolutionary disappearance of these structures among the higher primates and that the lack of callosities is not a primitive, but rather a newly acquired condition, which has progressed most among all catarrhines in man.

Friedenthal (1908) was the first author to report the occurrence of ischial callosities in chimpanzees. Lönnberg (1917), in describing a series of ten chimpanzees from the easternmost part of the Belgian Congo, states: "All the adult specimens are provided with very well developed ischiadic callosities." Lorenz von Liburnau (1917) mentions that an adult male chimpanzee from Central Africa (*Pan steindachneri*) possesses ischial callosities 7 cm. in diameter. The occurrence of ischial callosities in the so-called "Tschego" variety of chimpanzee has been reported by Sokolowsky (quoted by Schwalbe, 1923). Bolk (1926) found in a chimpanzee fetus, close to term, two entirely hairless, symmetrical zones over the ischial tuberosities, which he regards correctly as incipient callosities. The writer has observed the same hairless zones in one out of eight chimpanzee fetuses of closely corresponding ages. In a total of 94 chimpanzees (78 embalmed or fresh and 4 living specimens and 12 complete skins; ranging in age from birth to maturity), carefully examined by the author, horny ischial callosities were found in 36 specimens, or in 38 per cent of the cases. One such case is shown in Figure 3. These unquestionable callosities occur in both sexes, at all postnatal ages, and in wild as well as captive specimens; when present they can vary considerably in size and in regard to the thickness of actual horn formation.

Among 21 gorillas (14 embalmed, 5 living, and 2 complete skins) of varying ages the author has never seen any trace of these callosities, but Lönnberg (1917) mentions "ischiadic callosities in being" in *Gorilla beringei mikenensis*, consisting of thickened, bare zones on which "the horny layer has a tendency of peeling off in flakes." Among 61 orang-utans (22 embalmed specimens and 39 complete skins) of widely differing ages the author could discover callosities in only 3 cases (= 5 per cent); namely in one infant and in two



FIG. 3. PERINEAL REGION OF A JUVENILE CHIMPANZEE (Hopkins Coll. No. 387) SHOWING WELL DEVELOPED ISCHIAL CALLOSITIES (DRAWN by Mr. J. B. Wilson)

adults in which there existed clearly circumscribed, entirely hairless, and slightly thickened (but not really horny) areas overlying both ischial tuberosities. Friedenthal (1908) has pictured ischial callosities in an adult male orang-utan, but, judging by their corrugated surface, they can not have been really horny.

There can be no doubt that these structures, characteristic of all lower catarrhines and of all *Hylobatidae* (though in the latter they are in general comparatively small and appear late) persist in an atavistic manner in a great many chimpanzees and in an occasional gorilla and orang-utan, though in the last they are but faintly developed when present. In man alone have callosities never been

discovered and never will be since the ischial tuberosities have become completely padded by muscles arising from their entire surfaces, a condition restricted to man and preventing the skin from being pressed directly against bone. It is interesting to find that in regard to the frequency and development of ischial callosities man and chimpanzee stand much farther apart than man and orang-utan.

This conclusion is very similar to that derived from another observation on the perineal region, namely the periodic changes in the so-called sexual skin of females, which are very profound in chimpanzees and many lower catarrhines, whereas completely lacking in man, orang-utan and gibbon (Zuckerman, 1933). Quite recently it has become known that the female sexual skin of the gorilla also undergoes periodic changes, comparable to these changes in the chimpanzee (Raven, 1936, for mountain gorilla and Noback, 1936, for lowland gorilla). It should also be recalled in this connection that in regard to the *labia majora* and the urethro-vaginal tract Wislocki (1932) found a much greater resemblance between man and gibbon than between man and chimpanzee. Finally, it may here be mentioned that man and orang-utan are the only higher primates which can produce excessively long hair. In an adult male orang-utan the author found hair on various parts of the body exceeding 55 cm. in length, a dimension equalled only by the scalp hair of some human beings.

#### *Duration and Rate of Growth*

Man and the great apes have in common a striking tendency to prolong the period of growth. As shown by the data in Table 1, the duration of the prenatal portion of growth is in chimpanzee, orang-

utan and man from 41 to 66 per cent greater than in the representative of lower catarrhines, the macaque. The postnatal periods of growth have become even more lengthened in the highest primates when contrasted with the lower ones. This increase in the duration of the total period of growth is most pronounced in man and is possibly somewhat greater in the orang-utan than in the chimpanzee.

Based upon the data in Table 1 it can be calculated that of the entire period of growth, from conception to completed eruption of the permanent dentition, 6.2 per cent represent intrauterine life in the macaque, 5.6 per cent in the chimpanzee, and only 3.5 per cent in man. In other words, in relation to the total duration of growth man is born much more early than the chimpanzee or the macaque. In another study the author (1936) has demonstrated that at birth man is very much less advanced in his ossification than the macaque.

The figures in Table 2 show definitely that the relative increases in body weight are not closely correlated to the durations of growth. For instance, the human newborn is on an average more than twice as heavy as a newborn orang-utan, yet the duration of pregnancy is in man practically the same as in the orang-utan. The rate of prenatal increase in size is much greater in man than in the other higher primates. The rate of postnatal growth, on the other hand, is smaller in man than in the chimpanzee and, in all likelihood, the gorilla and the orang-utan. For these reasons the weight of the adult is many more times greater than that of the newborn in the large apes than in man. As shown in the last column of Table 2, the proportion between the body weight at birth and at maturity is very similar in man and the lower catarrhines,



whereas very dissimilar in man and the great apes.

These random notes, discussed so far, have already furnished some striking examples for the contention that man

tween man and orang-utan, or between man and gibbon, than between man and chimpanzee. It seems now desirable to consider specifically some of the conditions which have been selected by Weinert

TABLE 1  
*Tentative data for the durations of some periods of growth in different primates*

PRIMATE	DURATION OF PREGNANCY (CONCEPTION AGE)		AGE OF ERUPTION OF FIRST DECIDUOUS TEETH		AGE OF ERUPTION OF LAST PERMANENT TEETH	
	Absolute (Days)	Relative (Macaque = 100)	Absolute (Months)	Relative (Macaque = 100)	Absolute (Years)	Relative (Macaque = 100)
Macaque (Rhesus).....	166*	100	0.7	100	6.8*****	100
Gibbon.....	209**	126	0.9	129	unknown	?
Orang-utan.....	275***	166	4.5	643	unknown	?
Chimpanzee.....	235****	141	2.8	400	10.9	160
Man.....	266	160	6.5	929	19.9	293

All corresponding data for the gorilla are still lacking. \* = average of 26 viable newborns, after Hartman, 1932; \*\* = calculated from data by Ogilvie, 1923 (one case); \*\*\* = after Aulmann, 1932 (one case); \*\*\*\* = average of eleven records in recent literature, collected by Schultz and Snyder, 1935 (16 days have been deducted from average "menstrual age" to obtain approximate, average "conception age"); \*\*\*\*\* = average of most recent data by author (1936). The original data for the dental ages are reported in detail in another paper by the author (1935).

TABLE 2  
*Comparisons between body weights at birth and at maturity in different primates*

PRIMATE	AVERAGE WEIGHT OF NEWBORN		AVERAGE WEIGHT OF ADULT MALE		RELATION BE- TWEEN WEIGHT OF NEWBORN AND OF ADULT
	Absolute (grams)	Relative (Macaque = 100)	Absolute (grams)	Relative (Macaque = 100)	
Macaque (Rhesus).....	435***	100	9,152***	100	1:21
Langur.....	780**	179	17,000**	186	1:22
Gibbon.....	360**	83	5,900**	65	1:16
Orang-utan.....	1,500*	345	72,000**	786	1:48
Chimpanzee.....	1,600*	368	60,000*	656	1:37
Gorilla.....	1,800*	414	200,000*	2184	1:111
Man.....	3,200*	736	75,000*	819	1:23

\* = approximate averages, based upon data in the literature and some additional ones by the author (compiled in part by Schultz, 1927, 1930 b and 1933 b); \*\* = from weights of specimens in Hopkins collection; \*\*\* = averages according to Schultz, 1933 c. That the birth weight of gorilla has not been estimated too low is also evident from the notes by Brandes (1930).

possesses characters in regard to which he resembles the great apes less closely than the latter resemble one another. It has also been already indicated that certain features can differ to a lesser extent be-

(1932) as support for his claim that man has so many hereditary characters in common with the chimpanzee to warrant the conclusion: "... once there existed an anthropoid ape stem, of whose descend-

ants live to this day chimpanzee and man, whereas all other recent anthropoids had already become divided before this last separation and thereby had not any more acquired the chimpanzee—man—features." (literal translation.)

#### *Frontal Sinuses*

A large part of the book by Weinert deals with the frontal sinuses which are regarded as being of greatest significance for phylogenetic deductions since they are claimed to be strictly hereditary features and supposedly not needed for any particular function. Weinert states categorically: "Whereas no orang-utan possesses frontal sinuses, there exists no gorilla and no chimpanzee which is without these sinuses. The frontal sinuses are, therefore, really a feature which divides the anthropoid apes very sharply and without any overlapping of the ranges of variation; but not only that. The more primitive members of the anthropoid apes, namely the gibbons and orang-utans, conform to the condition in the lower primates; the other members, gorilla and chimpanzee, show the same formation as man." After having compared the size and shape of these sinuses in man and the African apes Weinert proceeds: "We must draw the conclusion that the best ancestral form of frontal sinuses is still found in the chimpanzee of to-day and that from this form evolved in diverging directions the frontal sinuses of gorilla and of man." (literal translation.)

Weinert's account of these supposedly very definite and, in that case, phylogenetically quite important conditions requires some corrections. In 1908 Cunningham had already reported the occurrence of a small frontal sinus in an adult orang-utan. In his original paper on frontal sinuses Weinert (1926) describes the conditions in orang-utan as follows:

"Measured from the lower border of the *Pars orbitaria* of the frontal bone, the cavity reaches on an average for 5 to 10 mm. up into the frontal bone and thus forms, if one wishes, a small frontal sinus. In an old male I measured once more than 2 cm., whereby the cavity had reached nearly to the upper orbital edge." (literal translation.) Finally, Kleinschmidt (1933) has published a detailed account of frontal sinuses in four orang-utan skulls (one of these cases is reproduced in Figure 4). Some of these rare sinuses in orang-utans reach higher up into the frontal bone than these sinuses do in occasional human beings, in whom they may not even approach the glabellar region, but lie in the frontal portion of the medial orbital walls (see e.g. Schaeffer, 1920, Figure 123). In Kleinschmidt's orang-utan No. 5 the portions of the sinuses surrounded by the frontal bone are certainly larger than the corresponding portions of the vestigial sinuses in the chimpanzee, shown in Figure 4. Furthermore, the skull of the adult pygmy chimpanzee (*Pan paniscus*), described by Coolidge (1933), contains only an extremely diminutive frontal (?) sinus, reaching at best very little above the lower edge of only the orbital part of the frontal bone. Finally, in man the frontal sinuses are known to be totally absent in very rare cases among the higher races, but, according to Turner (1901), in 30.4 per cent of Australian aboriginals.

It is quite evident from these notes that a trend for the formation of frontal sinuses is manifest in man and all the great apes, including the orang-utan, but that this tendency is least pronounced in the orang-utan and possibly no more so in pygmy chimpanzees. The differences in regard to frontal sinuses, existing among the great apes and man, are purely quantitative and relate merely to frequency of

occurrence and size and location of structure. It is well known that the size of the sinuses in man can vary between total absence and such enormous figures for cubic contents as easily surpass any maximum values for chimpanzee. The story of the frontal sinuses is in accord with the general assumption of a common origin

of hair man resembles the three great apes much less than the latter resemble each other (Schultz, 1931a), or the findings that among all higher primates man alone lacks sinus hairs (Friedenthal, 1908), that curly hair is a human peculiarity, that man is the only primate with *ossicula mentalia* in the mandibular sym-

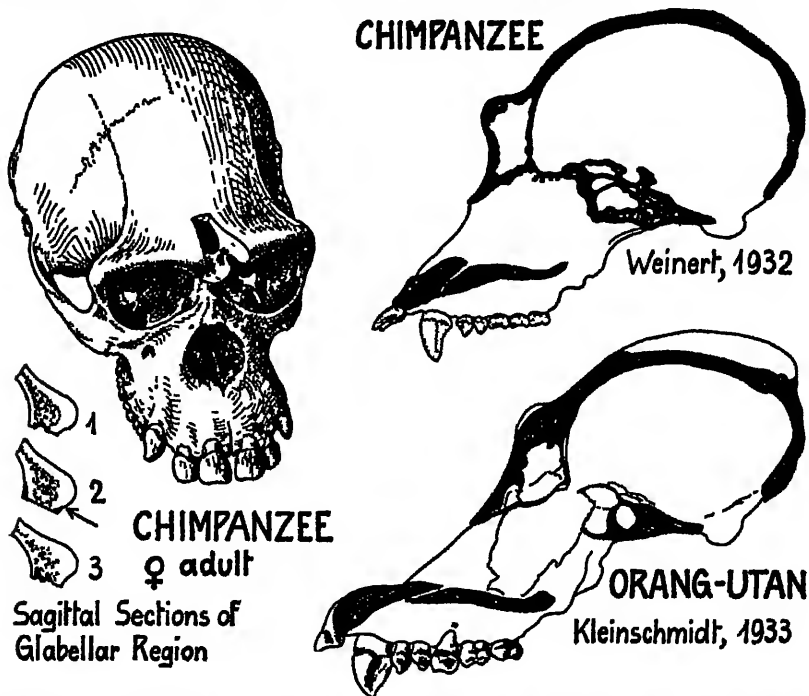


FIG. 4. LEFT: SKULL OF SMALL, BUT ADULT, FEMALE CHIMPANZEE FROM UNKNOWN LOCALITY (Labot. Phys. Anthropol., Hopkins Univ.) WITH BLOCK OF BONE REMOVED FROM GLABELLAR REGION TO SHOW THE DIMINUTIVE FRONTAL SINUS

Sagittal sections: 1 = 3 mm. medially from left end of block; 2 = midsagittal plane (arrow points to nasion); 3 = right end of block; 1 and 3 show the upper ends of the left and right sinuses.

RIGHT: MIDSAGITTAL SECTIONS OF SKULLS OF (ABOVE) CHIMPANZEE (PRESUMABLY OLD MALE) AFTER WEINERT (1932, FIG. 10), SHOWING ENORMOUS FRONTAL SINUS, AND (BELOW) OLD MALE ORANG-UTAN AFTER KLEINSCHMIDT (1933, FIG. 5), SHOWING AN UNQUESTIONABLE FRONTAL SINUS

for man and all the great apes, but does not prove Weinert's specific claim that chimpanzee and man were the last higher primates to separate. That man resembles most closely the chimpanzee in regard to merely the *average size and shape* of the sinuses carries no greater weight phylogenetically than, e.g., the fact that in regard to the general density and amount

physis of newborns, that only man possesses a transverse metatarsal ligament between toes I and II (Jones, 1919), and that a true inguinal ligament is exclusively a human character (Stewart, 1936).

#### Wrist Bones

After having given the usual and well-known account of the *os centrale* in pri-

mates, Weinert concludes: "... since normally the anlage of an *Os centrale* is not any longer present in gorilla, chimpanzee and man, this loss can be attributed only to a modification in their original inheritance, a change which took place only *once* and which to this day concerns gorilla, chimpanzee and man. The branch of the orang-utan was not affected by this loss, it must hence have become separated earlier and could not any more participate in the evolution of man." (literal translation.)

this carpal element. Leboucq (1884) mentions two cases of *Hylobates leuciscus* in which there is no free *os centrale*, but merely a nodule on the *naviculare* which may correspond to the *centrale*. In another specimen of this same species (a Java gibbon and not a siamang, as pointed out by the writer, 1933a) Boltze (1926) found the *centrale* to be completely fused with the *naviculare*. In an old siamang, finally, the author discovered complete fusion between the latter two bones on one hand (see Figure 5) and nearly complete fusion

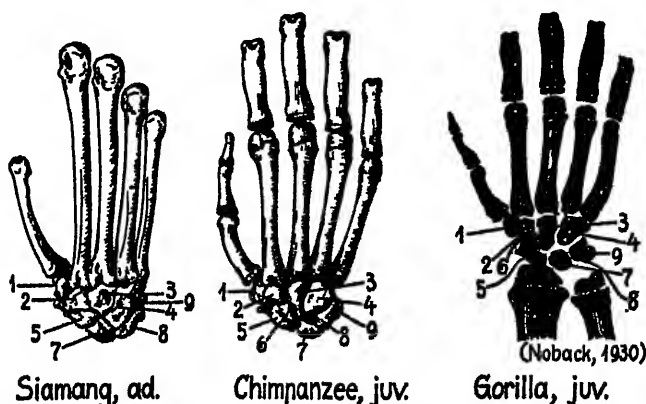


FIG. 5. LEFT: DORSAL VIEW OF WRIST AND METACARPUS OF AN OLD SYMPHALANGUS SYNDACTYLUS (Author's Coll.) WITH COMPLETELY FUSED (OR LACKING?) *Os centrale*; MIDDLE: HAND SKELETON OF JUVENILE CHIMPANZEE (Hopkins Coll.) WITH *Os centrale*; RIGHT: HAND SKELETON OF JUVENILE GORILLA WITH *Os centrale* (after X-ray photograph by Noback, 1930)

1 = *multangulum majus*, 2 = *multangulum minus*, 3 = *capitatum*, 4 = *hamatum*, 5 = *naviculare*, 6 = *centrale*, 7 = *lunatum*, 8 = *triquetrum*, 9 = *pisiform*.

The following compilation of old and new facts will demonstrate that Weinert's conclusions again require some very significant corrections. Among *Hylobatidae* the *os centrale* has been reported to be totally lacking, or else completely fused, in a considerable number of specimens. Thus, Lucae (1865) has figured a *Hylobates leuciscus* without an *os centrale*. Giebel (1879) states that among higher primates, including the gibbon, the orang-utan alone possesses the *centrale*, so it must be assumed that this careful observer happened to examine a gibbon without

on the other hand. It is, unfortunately, impossible at present to determine adequately the relative frequency of fused (or lacking?) central bones in *Hylobatidae*. Boltze observed this condition in one out of three adult specimens and the writer in one out of six skeletons, specially examined for the carpus, but the latter series contains two juveniles in which fusion is less likely to occur than in fully adult or old animals.

That the *os centrale* can fuse completely with the *naviculare* in the orang-utan, has been shown by Leboucq (1884), who

describes this condition in the ligamentous carpus of an adult. Incidentally, in a detailed study Virchow (1929) has demonstrated that the *os centrale* of orang-utan stands in regard to its topographic relations between the lower catarrhines and man.

As the disappearance of a free *os centrale* in the Asiatic anthropoid apes is most likely to occur in old specimens, so the persistence of this ossicle in the African apes is most apt to be encountered among very young animals. For the gorilla such persistence of a free *centrale* in each hand has been reported by Noback (1930), who found this carpal element by means of X-ray photographs in a living, healthy animal of the estimated age of 42 months (see Figure 5). In a chimpanzee of very similar age (all first permanent molars fully erupted) the author found a free *centrale*, containing only a very small ossification center, on the right hand (see Figure 5) and an entirely cartilaginous *centrale*, fused with the *naviculare* at its proximal and dorsal end, on the left hand. In another chimpanzee (author's collection) of the same dental age there exist on both hands between *multangulum minus*, *capitatum* and *naviculare* cartilaginous nodules which are partly fused with the navicular bones. That these nodules represent the central bones at a stage of belated fusion appears unquestionable, since no corresponding structures were present in five additional infantile and seven juvenile chimpanzees which had been examined by the author before they were macerated. Hartmann (1883) found in a "very young" chimpanzee the articular surface of the *naviculare* to be segmented by two transverse furrows, though the bone contained only one ossification center. In the light of the above facts it seems quite possible that this constitutes nearly completed fusion of the *centrale*. In three

chimpanzee fetuses of the Hopkins collection, corresponding in development to human fetuses of the seventh and eighth lunar month, there exists an *os centrale* in every case, as shown by Figure 6. In two of these fetuses the *centrale* is entirely free (in *A* it is very small and was hidden from view until the dorsal part of the *naviculare* had been removed); in the third fetus (*B*) the cartilages for *centrale* and *naviculare* are incompletely separated by a cleft, i.e., fusion has started at the proximal end of the *centrale*. Such clefts,

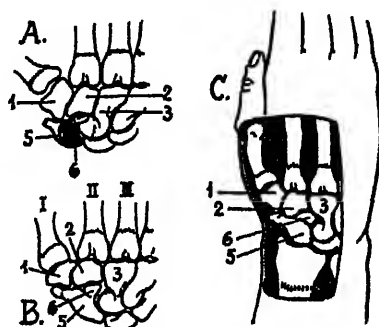


FIG. 6. SEMI-DIAGRAMMATIC SKETCHES OF THE DORSAL ASPECT OF THE RADIAL PORTION OF THE ENTIRELY CARTILAGINOUS WRIST BONES IN CHIMPANZEE FETUSES OF THE HOPKINS COLLECTION

*A* = No. 302; 214 mm. sitting height. The dorsal half of the *naviculare* (indicated by dotted line) has been cut away (at shaded area of "5") to show the hidden *centrale*. *B* = No. 390; 225 mm. sitting height. *C* = No. 394; 250 mm. sitting height. Numbers for the wrist bones as in Figure 5.

indicating incomplete coalescence between *centrale* and *naviculare*, have been found in a number of adult human skeletons (e.g., Pfitzner, 1895, Figs. 9, 12 and 13; Virchow, 1929, Fig. 24; Forster, 1933/34, Figs. 4, 5 and 6). The frequency of the persistence of entirely free central bones in adult man differs between a mere fraction of one per cent and three per cent according to different authors.

From the investigations of Rosenberg, Leboucq, and others we know that the *os centrale* appears regularly in the human embryo and that, as a rule, it fuses com-

pletely with the *naviculare* during the third month of prenatal life. From the notes assembled above it appears most probable that in chimpanzee (and gorilla?) this fusion between *centrale* and *naviculare* does not begin until late in fetal life. Indeed, it seems possible that the *average* age of completed fusion lies in the infantile period. Very few hand skeletons of chimpanzee and gorilla infants have been thoroughly examined before maceration, i.e., before the frequently cartilaginous and diminutive *centralia* might become lost or dried and shrivelled beyond recognition, yet we already possess two records of free and one of incompletely fused central bones in animals at least three years old. In orang-utan and, particularly, in the *Hylobatidae* the *centrale* can fuse with the *naviculare* during middle or old age. In lower catarrhines the author has never found such fusion, even in skeletons of very old animals, and has never seen a report describing such cases. It appears, therefore, that the various higher primates have in common a tendency to fuse the *centrale* with the *naviculare*, but differ quantitatively in regard to the age at which this tendency manifests itself and in regard to the proportion of individuals affected by this tendency at the differing ages. To the student of growth the difference between the ages of fusion of the *centrale* in man and in chimpanzee (very early and, at least, late intrauterine development) is as significant as the difference between the ages of fusion in chimpanzee and gibbon (late fetal or infantile life and old age).

Many normal growth changes in the skeleton differ very strikingly among the different types of catarrhines in regard to the relative ages at which they occur. For instance, the facial portions of the sutures between the premaxillary and maxillary bones disappear in man very

much earlier than in any other catarrhines. In the anthropoid apes the same tendency toward early obliteration of these sutures manifests itself in widely varying degrees, as has been abundantly demonstrated (e.g., Ashley-Montagu, 1935). The suture between the two nasal bones obliterates during fetal life in the macaque, usually during early juvenile life (occasionally not until late juvenile life) in the anthropoid apes, and in old age alone, and then only in very rare cases, in man; the metopic suture closes as a rule at comparatively later ages in man and the macaque than in the great apes; and the great fontanelle becomes closed at a much more advanced stage of growth in man than in any other primate (Schultz, 1936). The story of the *os centrale* is merely another instance of such differences in the ages at which skeletal growth changes take place, but this particular growth change, i.e., the tendency toward fusion between the two carpal elements, is clearly restricted to the higher primates.

There exist innumerable other conditions which reveal evolutionary trends common to all higher primates and at the same time have attained widely differing degrees of perfection in the various types. Obviously, Weinert has selected and over-emphasized conditions which happen to have reached more or less similar phylogenetic levels in man and the African apes, and he has grossly neglected many other conditions in regard to which man stands removed from chimpanzee and gorilla.

#### *Coccygeal Vertebrae*

Extreme reduction in the number of segments of the caudal portion of the spinal column exists in all the higher primates, but this evolutionary specialization has progressed to different extremes in the various genera. Weinert states

in this connection: "Gorilla and chimpanzee have as a rule five coccygeal vertebrae, man four, and the two Asiatic anthropoids only three. . . . Man can not have descended from gibbon or orang-utan, not have branched from a form which has fewer tail vertebrae than he himself; it is impossible that a rudimentary structure, which has already become reduced in its entirety, is subsequently again enlarged in man; i.e., increased by one vertebra. Gorilla and chimpanzee, however, show in the total composition of their spinal column, including the tail, a picture which is not only possible, but can have been expected, as a step preceding the conditions in man" (literal translation). For those who believe in the absolute irreversibility of evolution this might sound convincing, though it should be remembered that in embryonic life man still possesses 8 or even more caudal segments and that gibbon and orang-utan had ample time to reduce the number of their tail vertebrae *after* their separation from any line leading to man. The chief weakness, however, of Weinert's conclusions consists in the fact that his underlying data do not at all represent the typical conditions. These data are apparently copied from Fischer, who (even in a paper of 1933) states that his figures for the numbers of vertebrae in primates are in general based upon the data by Rosenberg, i.e., upon data which are far too scanty to furnish reliable averages. In 1930 (a) the writer published comprehensive statistics for the numbers of vertebrae in primates, which included the many scattered data from the literature as well as very considerable series of new records. The latter records have recently been combined with many new data by the author's colleague, Dr. W. L. Straus, Jr., who has kindly supplied the writer with the following new averages for the numbers of coccygeal vertebrae in anthro-

poid apes. These averages are based exclusively upon records of specimens in which there could be no doubt in regard to the exact number of true coccygeal vertebrae.

PRIMATE:	NUMBER OF SPECIMENS:	AVERAGE NUMBER OF COCCYGEAL VERTEBRAE:
Man.....	745	4.2
Chimpanzee....	47	3.2
Gorilla.....	69	3.0
Orang-utan.....	56	2.8
Gibbon.....	47	2.7
Siamang.....	13	2.6

If Weinert's sanguine reasoning were to be applied consistently to these new averages, one would have to draw the absurd conclusion that all the anthropoid apes originated from man-like ancestors!

It is significant that in regard to the number of coccygeal vertebrae man differs more from all the anthropoid apes than any two of the latter differ from one another.

#### *Relative Cranial Capacity*

As further support for his claim of the extremely close relationship between man and chimpanzee, Weinert gives a table of cranial capacities (cu. cm.), body weights (g.) and the proportions between the two. According to his figures the relation between the cubic contents of the brain case and the body weight equals among adults 1:40-60 in man, 1:150-200 in chimpanzee, 1:400-600 in gorilla, 1:300 (?) in orang-utan, and 1:100 in gibbon. Since the gibbon should not be compared on account of its small general size, Weinert points triumphantly to another instance of greatest resemblance between man and chimpanzee. If this particular proportion is to be used at all for phylogenetic deductions, it must be based either upon capacity and weight in the same individuals or else upon averages for

capacity and averages for weight which are derived from very extensive series of observations. The relation between cranial capacity (or the only approximately corresponding brain weight) and body weight varies enormously, chiefly on account of the latter factor. The age changes of this proportion are very profound since, particularly in apes, the brain increases comparatively little after infantile life, whereas the body weight can continue to rise very markedly even after growth in height has ceased. Incidentally, among newborns the orang-utan surpasses man in relative cranial capacity. The ratio between capacity and body weight equals in a newborn orang-utan approximately 1:7.7 and averages in newborn whites 1:8.6. These figures demonstrate also the tremendous post-natal changes in this ratio (adult man = 1:40-60).

In a previous paper the writer (1933a) has given the cranial capacities and body weights of large numbers of *Hylobatidae*. In the subgenus *Hylobates* alone the capacity of 77 adults averages 97.5 cu. cm. and the body weight of 52 adults averages 5900 g., resulting in a proportion of only 1:61 (instead of 1:100, as claimed by Weinert) for true gibbons. In an old male orang-utan (P.A.L. 101) the capacity is 450 cu. cm. and the body weight is 77.1 kg., thus the proportion amounts to only 1:171 and not to 1:300. In one of the two adult male orang-utans, carefully described by Milne-Edwards and others (1895), the capacity is 470 cu. cm. and the body weight is 65.5 kg.; the ratio, therefore, is only 1:139. For adult male chimpanzees an approximate, average ratio may be obtained from their average cranial capacity of 404 cu. cm. (Oppenheim, 1912) and their average body weight of 60 kg. (Table 2). The resulting ratio equals 1:149. In a practically adult (only

third molars not yet erupted) female mountain gorilla (P. A. L. 7) the capacity is 462 cu. cm. and the body weight is 72.6 kg.; the proportion between these data equals 1:157.

The ratio between the actual brain weight and the body weight averages quite approximately 1:50 in adult man and amounts to 1:114 in a very small, but adult, female chimpanzee (Fulton and Keller, 1932). It averages 1:112 in ten adult female orang-utans (Connolly, 1932), but equals 1:186 in a male orang-utan, weighing 73.5 kg. (Dubois, 1914). The giant male gorilla "Bobby" of the Zoological Garden in Berlin is reported to have had a body weight of 267 kg. and a fresh brain weight of only 610 g., i.e., a ratio between the two of 1:438. In the above mentioned female mountain gorilla this same ratio can not have been much over 1:175 (assuming that brain weight in g. equals approximately 90 per cent of cranial capacity in cu. cm.).

These figures suffice to show that the relation in size between brain and body does not separate the great apes to the extent, claimed by Weinert, since the enormous ranges of individual variations can overlap in all three types, particularly if both sexes are considered. If the most man-like ratio of the gibbon is excluded from these comparisons and quite properly regarded as partly due to the gibbon's small general size, then the ratio of giant male gorillas should also be omitted on account of its being influenced by extreme body size. There remains, therefore, only one safe and well established conclusion, namely that adult man possesses a relatively larger brain than other adult primates of similar body weights, i.e., orang-utans, chimpanzees and female gorillas. Differences in relative brain size among these great apes most likely exist in the *average* values, but are certainly not



as great as the difference between man and any of the anthropoids of comparable body weight.

### *Os Penis*

A rod-shaped bone of varying size occurs in the penis of all simian primates, except in some platyrrhines and in man. In very rare cases a penis bone can occur in man, but probably only as a pathological, rather than as an atavistic, formation (see e.g. Jacobi, 1899). Weinert (1932) pictures a small penis bone of an adult chimpanzee and a large penis bone of an adult orang-utan and states: "... it is again the orang-utan which, with its comparatively large bone, is farthest removed from man, whereas the chimpanzee, with the smallest ossicle, occupies again the nearest step." The following facts regarding the length of the penis bone in chimpanzee and orang-utan are compiled from the literature and from the author's own observations: Length of *os penis* in adult chimpanzee = 8.5 mm. according to Weinert (1932); 9 mm. in a sub-adult specimen (Hopkins coll. No. 392, 3rd molars not yet erupted) weighing 40.2 kg.; 10.5 mm. in an adult specimen (Hopkins coll. No. 206) weighing 43.8 kg. and measuring 48 inches from crown to heel; "a little more than half an inch long," i.e., at least 13 mm., in an adult, measuring 47 inches from crown to heel, dissected by Sonntag (1923). Length of *os penis* in adult orang-utan = 12 mm. according to Weinert; 12 mm. in another specimen, according to Pohl (1928); 15 mm. in a specimen, weighing 73.5 kg., described by de Pousargues (1895); "smaller than in de Pousargues' specimen" in two adults, one of which weighs 76.5 kg., described by Fick (1895); 11 mm. in a specimen (Hopkins coll. No. 212) weighing 77.1 kg. The last penis bone is at least as slender and pointed as those pictured by

Pohl and by de Pousargues and is not nearly as thick and blunt as the specimen pictured by Weinert.

It is readily seen that there exists no justification for concluding that the penis bone of the chimpanzee is appreciably smaller in proportion to the size of the animal than that of the orang-utan. We possess records on a chimpanzee with a penis bone at least 13 mm. long and on a fully grown orang-utan in which this bone measures only 11 mm. The latter animal weighs over 77 kg. and in a chimpanzee of only 44 kg. the penis bone is 10.5 mm. long.

These notes on the *os penis* add another instance to the list of characters which differ far more between man and any of the great apes than the latter differ among themselves. The complete lack of a penis bone, as the universal absence of ischial callosities and of sinus hairs, is at least among higher primates a specifically human character which removes man from as close a proximity to the chimpanzee as has been claimed by Weinert and others.

### *Kidney*

In a chapter dealing with the papillae of the kidney Weinert maintains that it is again the chimpanzee in which the conditions of man are foreshadowed. In a comprehensive and careful study of primate kidneys Straus (1934) has reached a quite different conclusion. He states: "He (Weinert) attempted to show that in the structure of the kidney (i.e. number of papillae), among other points, the chimpanzee more closely approaches Man than does any other Primate. A critical examination of the available evidence, however, shows plainly that neither the chimpanzee nor any other anthropoid ape can be regarded as suggesting the human form of kidney. Consideration of Primate kidneys from a phylogenetic aspect

merely emphasises the unique and isolated position of Man. The only approach to the human condition is made by the spider monkey, . . ."

#### *Menstrual cycle*

Weinert states that the chimpanzee and man have the same duration of the menstrual cycle, i.e., 28 days. According to all available information (collected by Schultz and Snyder, 1935) and on the basis of the latest records from the Johns Hopkins colony of living chimpanzees the writer is convinced that the *average* menstrual period of these apes amounts to considerably more than 30 days. A brief report by Tomilin (1936), which has just appeared, gives as average for 50 normal menstrual cycles of the chimpanzee 35.5 days. In orang-utan this period averages 32 days (Aulmann, 1932), whereas in the macaque 28 days (Hartman, 1932). It appears, therefore, that in regard to this feature man and macaque are alike, but differ from orang-utan and chimpanzee.

Weinert's work has been selected for this critical review merely because it represents one of the most ambitious and comprehensive attempts to determine man's exact place on the family tree of higher primates. Ample evidence has been discussed above to show that Weinert's widely accepted conclusions rest on many data which are at times insufficient and in part incorrect. The pertinent facts at our disposal justify the conclusion that *in general* man resembles somewhat more closely the African anthropoid apes than any other primate, but they do not justify the more specific conclusion of Weinert that the resemblance between man and chimpanzee is much closer than, or even as close as, the aggregate resemblance between the African apes and the orang-utan. There exists as yet no unimpeach-

able evidence for the assumption of Schwalbe and of Weinert (most recently also accepted by Gieseler, 1936), that man and chimpanzee have been the last higher primates to become phylogenetically separated and this at a comparatively recent date.

#### DEGREES OF RESEMBLANCE BETWEEN THE HIGHER AND THE LOWER CATARRHINES AND BETWEEN MAN AND THE ANTHROPOID APES

In an attempt to establish tentatively the degrees of resemblance between the various higher primates in regard to their quantitatively measurable characters it is essential to find a type of lower catarrhine which shows most closely (even though at best only approximately) the original and hence primitive conditions. The macaque can be regarded as the most suitable, generalized representative of the lower catarrhines. This conservative primate has had no share in the many, minor specializations in structure and habit which characterize most of the other forms of the *Cercopitheciinae* and all the genera of the *Semnopitheciinae*. At least in regard to the proportions of its outer body and those of its skeleton the macaque, particularly the Rhesus monkey, has probably deviated comparatively little from the conditions which we can assume to have existed in the ancestral type of lower catarrhine from which all later higher primates originated.

By expressing the quantitative characters of the higher primates in percentage of the corresponding conditions in the macaque, a method is obtained by which not only the direction of the approximate phylogenetic change becomes evident, but also the comparative degrees of evolutionary change in different characters as well as the relative amounts of

difference between the various higher primates.

### Spinal Column

The numbers of vertebrae in the different regions of the spinal column furnish

for man is 17.0, or 10 per cent smaller than in the macaque. If the former average is assumed to equal 100, the latter average will appear on the same scale at 90, and the corresponding average for the orang-utan (16.0) at 84.7. Figure 7

TABLE 3

The averages of the numbers of vertebrae in the thoracolumbar and sacral regions of the spine in different primates and the percentage differences between the averages of the Macaque and those of the other primates

PRIMATE	NUMBER OF SPECIMENS	THORACOLUMBAR VERTEBRAE		SACRAL VERTEBRAE	
		Average number of vertebrae	Percentage difference from Macaque	Average number of vertebrae	Percentage difference from Macaque
Macaque.....	53	18.9	0	3.0	0
Langur.....	49	19.0	+0.5	2.9	-3.3
Gibbon.....	81	17.9	-5.3	4.4	+46.7
Siamang.....	23	17.4	-7.9	4.5	+50.0
Orang-utan.....	83	16.0	-15.3	5.1	+70.0
Chimpanzee.....	63	16.8	-11.1	5.4	+80.0
Gorilla ( <i>G. gorilla</i> + <i>G. beringei</i> ).....	104	16.6	-12.2	5.6	+86.7
Man.....	3856	17.0	-10.0	5.2	+73.3

The data for the Langur have been kindly supplied by Dr. W. L. Straus, Jr., those for the Macaque, Orang-utan, Chimpanzee, and Man are from the author's paper of 1930 a, those for the Gibbon and Siamang from the author's paper of 1933 a, and those for the Gorilla from the author's paper of 1934.

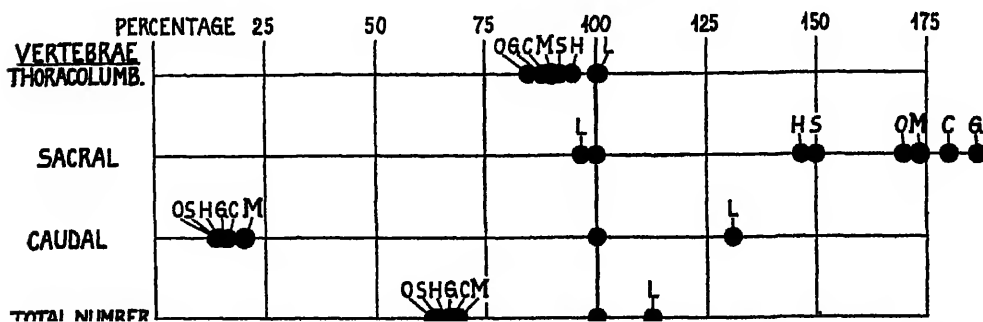


FIG. 7. DIAGRAMMATIC REPRESENTATION OF THE AVERAGE NUMBERS OF VERTEBRAE IN HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING AVERAGES IN THE MACAQUE

Explanation of the abbreviations in this and all following, similar figures: L = Langur, H = Gibbon, S = Siamang, O = Orang-utan, C = Chimpanzee, G = Gorilla (both species combined; in case the species are shown separately, G stands for only *Gorilla gorilla* and B for *G. beringei*); M = Man. The macaque is always shown on the perpendicular line, representing 100 per cent.

a simple example of this method for demonstrating the quantitative differences between various primates (see Table 3 and Figure 7). The average number of thoracolumbar vertebrae amounts to 18.9 in the macaque; the corresponding average

and all the following, similar figures are constructed according to this principle and by means of these simple calculations. Figure 7 shows very clearly that in regard to the numbers of vertebrae all the higher primates have become removed as one

group from the lower catarrhines, though the exact degrees of deviation differ in the various types. The numbers of thoracolumbar and of caudal vertebrae and the total numbers of all vertebrae have become reduced in the higher primates, as compared to the lower catarrhines, whereas the numbers of sacral vertebrae have become increased. The relatively greatest changes have occurred in the sacral and caudal portions of the spine. On the basis of the justifiable working hypothesis that the numbers of the vertebrae in the various regions of the spine are at most very little different in the macaque

numbers of his spinal segments. It is also very significant to find from Figure 7 that the differences between the two representatives of the two subfamilies of the lower catarrhines are always much smaller than the differences between either of the two and any of the higher primates.

Not only the numbers of the vertebrae are of interest in studying the resemblances between different primates, but also the relative lengths of the various regions of the spine. Table 4 contains preliminary data on these relative lengths, which were obtained by the author on fresh or embalmed bodies by measuring with a tape

TABLE 4

*Preliminary data showing the relative lengths of the various regions of the spinal column\**

ADULT PRIMATE	LENGTH OF SPINAL REGION IN PERCENTAGE OF TRUNK HEIGHT					
	Cervical	Thoracic	Lumbar	Thora-columbar	Sacral	Caudal
Macaque (Average of 5 <i>Pithecius rhesus</i> ).....	17.6	42.4	45.1	87.5	11.4	69.3
Gibbon, ♂.....	16.9	40.2	24.6	64.8	13.7	4.6
Orang-utan, ♂.....	24.1	49.8	23.9	73.7	27.9	6.2
Chimpanzee, ♂.....	23.5	51.1	17.2	68.3	29.4	8.6
Gorilla ( <i>beringei</i> ) ♀.....	23.7	49.8	27.7	77.5	26.4	9.2
Man (Average of 9 Negroes, 1 White, 1 Filipino).....	25.9	53.9	37.3	91.2	25.8	6.3

\* (Measured with tape between centers of intervertebral disks at ends of spinal regions) in different adult primates (all fresh bodies, except gibbon and orang-utan which had been embalmed).

(or in any other lower catarrhine, since they are all remarkably uniform in this respect) and in the common ancestor of all higher primates, it can be concluded that the phylogenetic change from the original condition has been smaller in man than in any anthropoid ape in regard to the number of the caudal vertebrae and the total number of vertebrae, that the change has been smaller in man than in the great apes in regard to the number of thoracolumbar vertebrae, and that it has been smaller in man than in the African apes alone in regard to the number of sacral vertebrae. Man, therefore, is revealed as comparatively primitive in the

along the ventral side of the intact spinal column between the centers of the intervertebral disks at the ends of each spinal region while the bodies were carefully placed flat on their backs to avoid changes in the curvature of the spine which stretch or compress the intervertebral disks. Even though the figures for the higher primates, besides man, are as yet based upon single specimens only, it can be stated that, in proportion to the anterior trunk height, the cervical region of the spine has become greatly lengthened in man and all three great apes in contrast to the macaque (and some other lower catarrhines, not listed in the table), the

thoracic region of all higher primates has become somewhat increased in length, whereas the lumbar region has become shortened to a slight extent in man and to a tremendous extent in the gibbon and the large apes. As is to be expected from the increase in the number of vertebrae participating in the formation of the sacrum of the higher primates, the relative length of the sacral region is much greater in man and the apes than in the macaque. In regard to the relative length of the thoracolumbar portion of the spine man and macaque are practically alike and stand in sharp contrast to the much lower figures for the gibbon and the great apes. In this respect, therefore, man differs much more from any of the great apes than the latter differ among themselves.

#### *Proportions of the Trunk and Neck*

By the same considerations and methods, as outlined above, the more significant body proportions have been calculated as percentage differences in relation to the conditions in the macaque. The absolute values of these proportions and their changes during postnatal growth have already been published by the author (1933 b) or will be recorded in future papers. The interest here is centered upon the relative differences between the proportions of different primates at birth and at the completion of growth. It may be merely mentioned that the relative differences between adults are based upon averages derived from measurements on two to nine specimens for each type of primate, whereas those between newborns are based only upon the data for single specimens, with the exception of man, who is represented by the averages of ten white and ten negro newborns. The methods, by which the measurements and their proportions have been obtained, are fully described in a special

paper by the author (1929). The anterior trunk height (from suprasternal notch to upper end of pubic symphysis) is most frequently employed in proportions which intend to free other measurements from the factor of general body size, because it is by far the most suitable and accurate dimension that can be chosen for comparative studies on primates.

The first proportion in Figure 8, the relative chest circumference, amounts in the newborn macaque to 138.8 and in the newborns of higher primates to anywhere between 168.6 and 208.4. The latter values equal from 121.5 to 150.2 per cent of the value in the macaque and appear as these percentages in Figure 8. In the adult macaques the relative chest circumference has decreased on an average to 103.0 and the averages of the adult higher primates fluctuate between 148.8 and 223.4, i.e., between 144.5 and 216.8 per cent of the average in adult macaques. These examples suffice to illustrate the precise construction of these diagrams for the relative differences in body proportions.

All the proportions of the trunk and neck, shown in Figure 8, separate the higher primates from the lower catarrhines and demonstrate that the former have departed from the conditions in the latter in one and the same direction, but this to widely differing degrees. In regard to all these proportions the adult higher primates deviate more from adult macaque than the newborns of the former deviate from newborn macaque. Already at birth, however, are the differences between the higher and the lower forms clearly apparent, these differences becoming merely more accentuated during postnatal growth. In comparison with the macaque, or langur, in all higher primates the chest girth is relatively much greater, the shoulders and hips are

proportionately much broader, the chest is markedly wider in relation to its depth, and the neck is relatively much longer. Of all these proportions the relative chest girth and the relative shoulder breadth show the most striking differences between higher and lower primates and we may assume, therefore, that the most profound evolutionary alterations consist in a widening of the

more conservative than those of, e.g., the gorilla.

#### *Position of Nipples*

Adult man has the lowest placed nipples among all simian primates. The vertical position is accurately expressed by the percentage relation between the distance from the level of the nipples to the upper edge of the pubic symphysis and

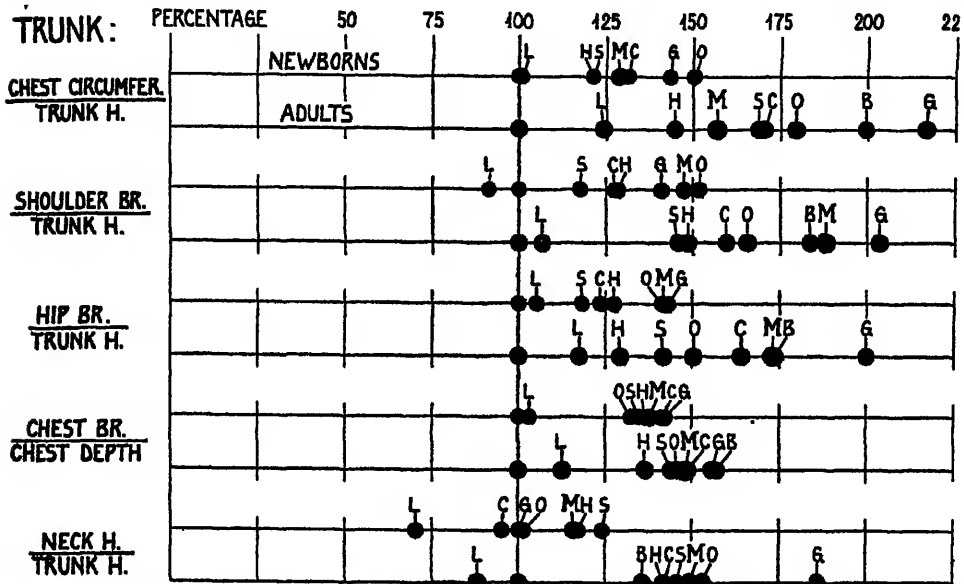


FIG. 8. DIAGRAMMATIC REPRESENTATION OF THE PROPORTIONS OF THE TRUNK AND NECK IN NEWBORN AND IN ADULT HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING PROPORTIONS IN NEWBORN AND IN ADULT MACAQUE

For each proportion the conditions in newborns are shown on the top line and those in adults on the slightly heavier bottom line. For explanation of abbreviations see title of Figure 7. N.B. The macaque always appears on the perpendicular line "100."

chest and a broadening of the shoulders. In regard to his trunk and neck proportions man stands among adults nearest to the mountain gorilla in two instances, nearest to the chimpanzee in one instance, nearest to the orang-utan in one instance, and nearest to the gibbon in the remaining instance. In none of these proportions does man show an extreme departure from the condition in the macaque; indeed, the human trunk proportions are much

the trunk height. This index averages 80 in macaques, 84 in gibbons, 90 in orang-utans, 86 in chimpanzees, 82 in gorillas, whereas only 76 in man (Schultz, 1933b, Table 8). The horizontal position of the nipples is shown by the percentage relation between the distance from right to left nipple and the chest breadth. This index averages 40 in macaques, 32 in gibbons, 28 in siamangs, 89 in orang-utans, 52 in chimpanzees, 46 in

gorillas, and 71 in man. Compared with the conditions in the macaque, the nipples have descended in man (for 4 index units), whereas ascended in the anthropoid apes (for 10 index units in orang-utan); they have moved farther apart in all great apes and man, but this to only a moderate degree in the African apes, to a very marked extent in man, and to the most extreme degree in the orang-utan. It is most significant that the horizontal and vertical locations of the nipples are remarkably uniform in all the many lower catarrhines in contrast to the higher primates among which the nipples have

hence most likely phylogenetically. In the quadrupedal catarrhine monkeys the relative shoulder height is very much smaller than in any of the anthropoid apes (Schultz, 1933 b, Table 8).

### Sternum

The tremendous phylogenetic increase in the stoutness of the trunk of higher primates has been associated with many other changes. Thus, the shoulder blades have migrated from the side to the back of the thorax, the spinal column has shifted more or less toward the center of the thorax (by far the most in man), and

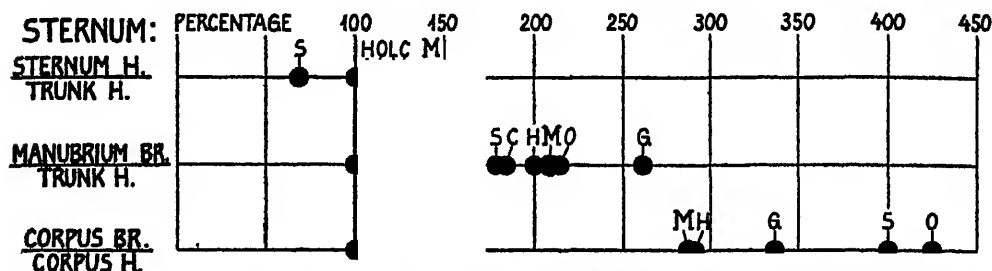


FIG. 9. DIAGRAMMATIC REPRESENTATION OF SOME PROPORTIONS OF THE STERNUM IN HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING PROPORTIONS IN THE MACAQUE

The figures for the relative breadth of the *corpus sterni* are from Schultz (1930a, Table 14) and those for the other two sternal proportions are from as yet unpublished measurements by the author on the following adult specimens, in all of which the trunk height was measured before maceration of the skeleton: 6 Rhesus monkeys, 1 Langur (*Pygathrix entellus*, ♂), 1 Gibbon (*Hylebates lar*, ♂), 1 Siamang (*Symphalangus syndactylus*, ♂), 1 Orang-utan (♂), 3 Chimpanzees, 3 Gorillas, and 6 Men. Abbreviations explained in title of Figure 7.

shifted in widely differing degrees and even in opposite directions.

### Height of Shoulders

In all the anthropoid apes the shoulders lie high above the suprasternal notch, so that the clavicles diverge upward. The chimpanzee possesses the most extreme, average, relative shoulder height, even though it is not nearly as pronounced a brachiator as the Asiatic anthropoids. In contrast to this, the clavicles of adult man are practically horizontal in a position of rest, i.e., the shoulders have descended to the level of the upper end of the sternum and this ontogenetically and

the sternum and the pelvis have followed by the increase of their transverse diameters the widening of the entire trunk.

Some of the generic differences in the proportions of the sternum are shown in Figure 9. The total height of the sternum (*manubrium* + *corpus* height) in relation to the height of the trunk differs comparatively little in the higher and in the lower catarrhines, though in man and gorilla the sternum is relatively longer and in the siamang relatively shorter than in the macaque. The relative breadth dimensions of the sternum are the ones which have become greatly increased in all higher primates in striking contrast

to all the lower catarrhines, so that the former are sometimes referred to as the *latisternal* primates. The breadth of the *manubrium* in relation to the trunk height is more than two and a half times greater in the gorilla than in the macaque and the breadth of the *corpus* in relation to the height of this sternal segment is more than four times as great in the orang-utan than in the macaque. As in the general trunk proportions, so in the sternal proportions, is it apparent that man has not reached the extreme development of some other higher primates. In regard to one of the proportions in Figure 9 man stands nearest to the gorilla, in regard to another nearest to the orang-utan, and in regard to the third nearest to the gibbon.

In contrast to the lower catarrhines, all higher primates have a general tendency toward fusion of various segments of the sternum, but this is much less

pronounced in orang-utan and gorilla than in chimpanzee and, particularly, man. In many gibbons and some gorillas and chimpanzees the uppermost segment of the *corpus sterni* fuses with the *manubrium*, whereas in orang-utan and man this occurs at best only in very old age. In regard to the comparatively early fusion of the various portions of the *corpus sterni* man is most closely approached by the chimpanzee, though there remain some significant differences (Schultz, 1930 a).

The very fact, that according to each single one of these features the higher primates are arranged every time in different sequences, makes it appear most prob-  
able that all the major representatives of  
this natural group have become separated in early and rather rapid succession after having inherited the same general evolutionary trends from their common ancestor.

(To be continued)





# THE PROBLEM OF CYCLOPIA

## PART II

By HOWARD B. ADELMANN

*Department of Histology and Embryology, Cornell University, Ithaca, N. Y., and Department of Ophthalmology, Columbia University, New York City*

### IV. NEWER ASPECTS OF THE PROBLEM OF CYCLOPIA

HAVING considered the question of the prospective significance of the eye-forming areas of the anterior end of the neural plate, the time when the ability to differentiate independently as an eye is first acquired by the cells in that region and the factors influencing the localization of eye-forming potencies, we may now consider the application of these facts to the problem of cyclopia. In this connection the question of the relation between the prospective significance and the prospective potencies of the eye-forming regions remains to be considered. Two possibilities suggest themselves. (1) The eye-forming materials of the neural plate may be rigidly determined, a strict correlation between prospective significance and prospective potency existing. (2) The eye-forming materials as late as the early neural plate stage may constitute a harmoniously equipotential system, any part of which is capable of forming any part of the optico-ocular apparatus.

#### *Equipotentiality of Presumptive Medullary Plate*

Spemann and Bautzmann ('27) have shown that until relatively late stages of gastrulation the presumptive medullary plate, particularly in its anterior portions, constitutes a harmonious equipotential system. In each of two eggs of *Triton*

*taeniatus* lateral segments of the eggs were cut off by a section which passed to the left of the midline in one member of the pair and to the right in the other. The two smaller segments and the two larger were then healed together so that eggs lacking a median strip and eggs possessing an excess of median material were produced. Thirty-eight of 46 embryos which lacked median material and which were operated on in stages ranging from the horseshoe-shaped to the slit-like blastopore stage, possessed normally proportioned forebrains and eyes. The remaining cases were too young for a decision to be made, or were necrotic or abnormal. No cases of cyclopia were observed. In many cases the embryos possessing superfluous material showed complete regulation of the anterior end.

So far as the presumptive medullary plate is concerned, the problem is therefore solved. The material out of which the tapetum, retina, optic stalks and chiasma will later differentiate is harmoniously equipotential. Material, the prospective significance of which is to form retina may form other parts of the optico-ocular apparatus and vice versa. It is to be noted, however, that in these experiments the entomesoderm or substrate was also involved and the experiments indicate considerable regulative ability on the part of the ectoderm and, particularly, the anterior part of the substrate. The marked regulative capacities of the latter are also borne out in

experiments of Roux ('88), Lehmann ('26), and Holtfreter ('33a) among others. Since the ectoderm alone from the eye-forming region transplanted from a stage well before the oldest utilized by Spemann and Bautzmann will differentiate into a well formed eye (Mangold, '28) we may assume that the ectoderm alone is harmoniously equipotential.

Recent experiments seem to indicate that the equipotentiality of the eye-form-

two eyes of considerable size were formed in 11 of 26 cases and absent in only four (fig. 23). The removal of a lateral third of the neural plate results in the formation of a rudimentary optic vesicle on the operated side, but if the antero-posterior extent of the defect is not great enough an eye of practically normal proportions may be formed (Adelmann, '29a). To prevent completely the formation of an eye the defect would have to extend almost

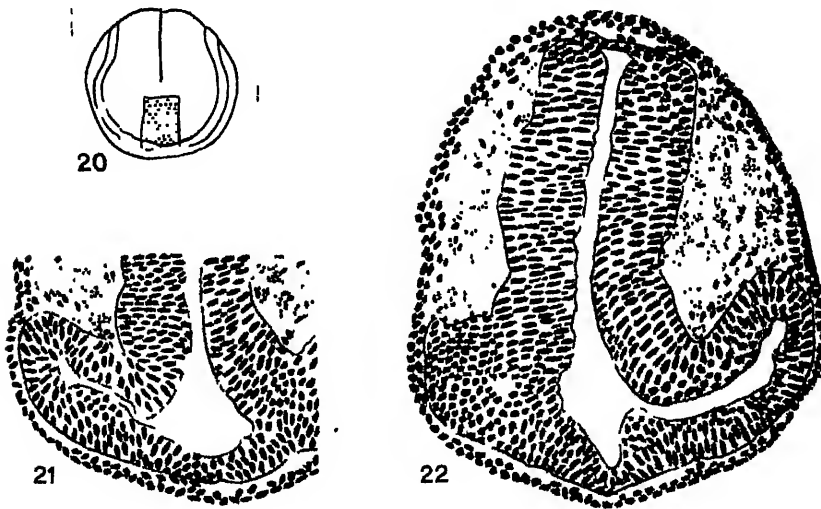


FIG. 20. CAMERA LUCIDA DRAWING OF AN EARLY NEURAL PLATE STAGE OF *AMBLYSTOMA PUNCTATUM* FROM WHICH A MEDIAN STRIP HAS BEEN REMOVED  
The excised area is stippled

FIGS. 21-22. DRAWINGS OF SECTIONS THROUGH THE OPTIC VESICLES OF EMBRYO FIXED TWO DAYS AFTER THE OPERATION SKETCHED IN FIGURE 20. (ADELMANN, '29)

ing areas of the neural plate persists as late as the neural plate stage in the amphibia. Adelmann ('29a, b) found that the removal of a median strip about  $\frac{1}{3}$ - $\frac{1}{4}$  of the greatest width of the neural plate of *Amblystoma* did not prevent the formation of two eyes (figs. 20-22). In the majority of cases (9 out of 12) brain and eyes were regulated to form a harmonious whole. This has been confirmed by Mangold ('31) who found that after the removal of a median strip as broad as  $\frac{1}{2}$  the greatest breadth of the neural plate,

or quite to the midline and back as far as the broadest portion of the neural plate. This is in accordance with the findings of Wachs ('20), who demonstrated, further, that a small eye formed after the removal of a lateral segment of the medullary plate may subsequently attain normal size and structure. A similar restitution was also noted by Mangold ('31). When two-thirds of the anterior end of the neural plate are removed, the remaining lateral third gives rise to an eye which may equal the normal proportions (Adelmann, '29a).

The experiments of Adelmann and Mangold may be contrasted with those of Stockard ('13c) who found that 45 per cent of nine embryos from which a median strip of the neural plate had been removed failed entirely to develop eyes, four others had defective eyes. In 80 per cent of 30

In spite of these differences the experiments of Mangold and Adelmann indicate that the eye-forming potencies of the anterior end of the neural plate are more or less diffusely localized and extend beyond the bounds of the presumptive anlage as defined by Manchot and Woerde-

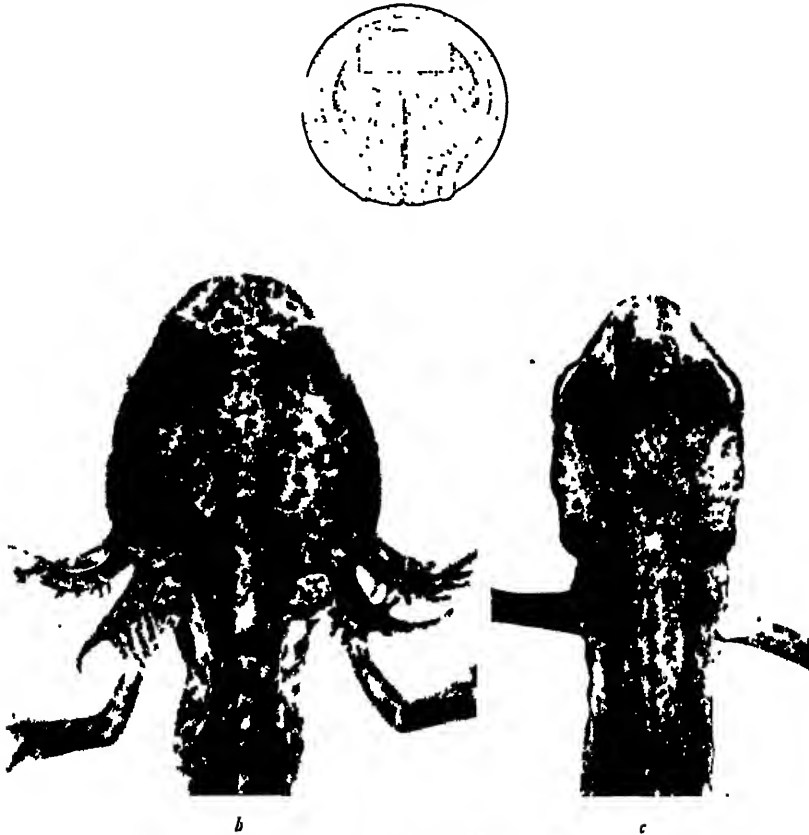


FIG. 23. RESULTS OF THE EXTIRPATION OF A BROAD MEDIAN AREA OF THE NEURAL PLATE IN *TRITON TAENIATUS*

(a) A piece  $\frac{1}{2}$  of the length and  $\frac{3}{4}$  of the width of the cephalic portion of the neural plate is removed. (b) Seventeen days after the operation, two eyes are present, the right about  $\frac{1}{2}$  the size of the left which is of almost normal size. (c) Head of the metamorphosed animal, 103 days after the operation. The right eye has been regulated to almost normal size. (Mangold, '31).

embryos from which lateral portions of the neural fold had been removed, both eyes were formed. The difference may, perhaps, be explained on the basis of age-differences in the material used, variation in the width of the strips removed, or possibly individual differences in the extent of the eye anlage in different strains.

man, a conclusion also reached by Mangold ('28). They demonstrate, further, that cyclopia cannot be produced in the urodele by simple excision of even a relatively broad median area of the neural plate (as great as  $\frac{1}{2}$  the greatest width, Mangold, '31) as one might expect if there a strict determination of parts. Both

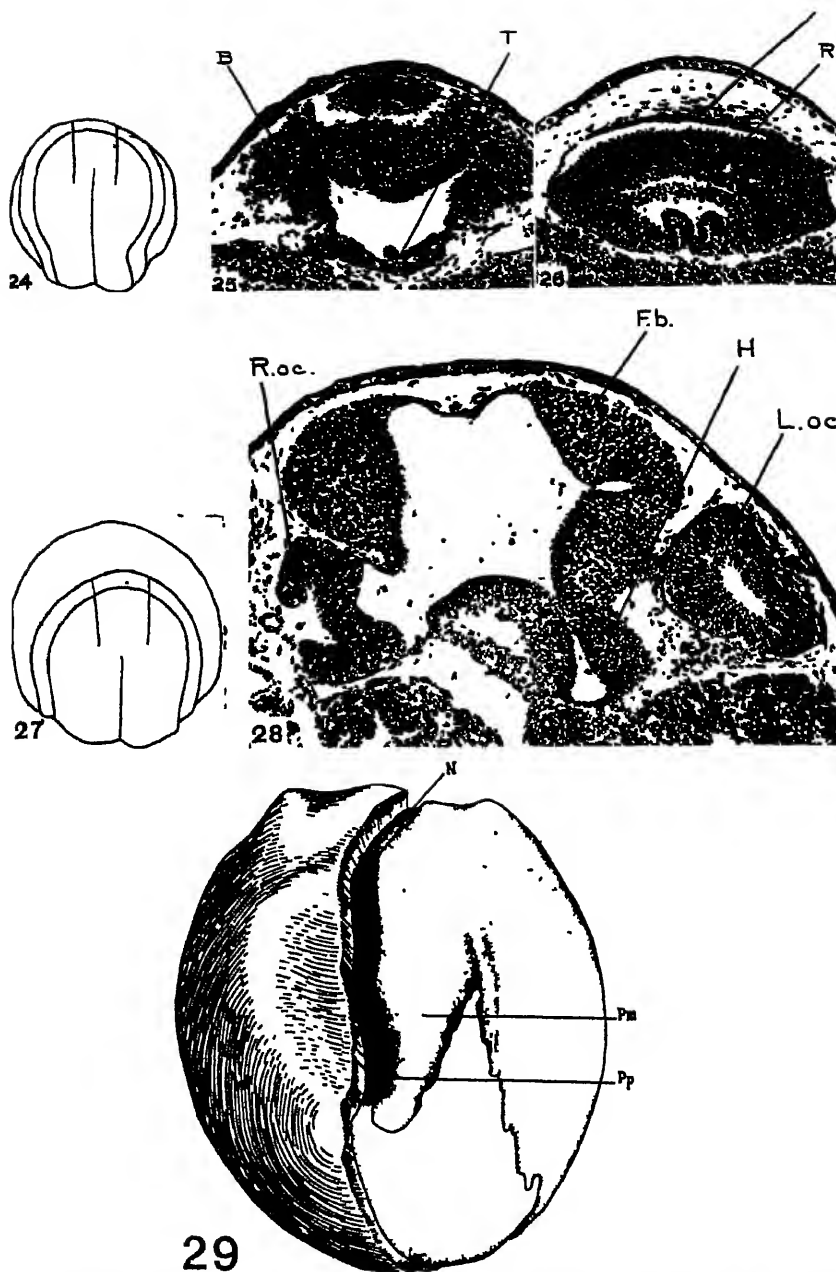
Adelmann and Mangold conclude that in the case of median defects, a regulation between brain and eye, especially in the transverse diameter of the plate, is possible. Daltrop ('32) has recently shown, however, that in the case of lateral defects reaching to the midline, the regulation and restitution of the brain are affected almost entirely by the utilization of material situated caudal to the defect, the material on the normal side aiding only in restoring the dorsal portions of the reconstituted brain. In its ventral portions the intact side is drawn out laterally in accordance with its normal movements. Since, however, the ventral portions of the forebrain, and diencephalon may be replaced by prospective hindbrain material of the operated side, her results do not prove that the ventral parts of the forebrain and midbrain on the intact side lack the ability to replace the ventral portions of their counterparts on the operated side, but that when left in situ their normal shiftings prevent them from doing so. Daltrop's experiments do not prove that in the case of a purely median defect, all of the restitutive tissue comes from the caudal edge of the wound.

*Eye-forming Potencies Higher Medially than Laterally*

Transplantation of median and lateral areas of the anterior end of the medullary plate yields further evidence as to the properties of the eye-forming materials. In transplants of median and lateral thirds of the anterior end of the neural plate of *Amblystoma*, without the underlying roof of the archenteron, into the belly wall of older hosts, Adelmann ('30) found that over six times as many eyes were differentiated from median as from lateral strips. The eye-forming potencies of the median regions of the neural plate alone are therefore much greater than those of the more lateral regions. The median strips in all

cases differentiated into perfectly single eyes often resembling cyclopean eyes in their relation to the implanted brain (figs. 24-26). Such eyes are attached to the brain by tapetum and there is an entire absence of any structure which may be interpreted as chiasma. Furthermore the donors of median tissue which differentiated as an eye often possessed a normally proportioned brain and eyes. In one case the donor formed one eye from the right lateral third of the anterior end of the neural plate left in situ, while eyes were formed from both median and left lateral strips when transplanted from the same donor. The experiments as a whole indicate that the various regions of the optico-ocular apparatus (i.e., the primitive chiasma, the optic stalks, retina and tapetum) are not rigidly determined in the neural plate itself in the early neural plate stage of *Amblystoma*. This is especially clear from transplants of median strips in which a single cyclopean-like eye was differentiated from the region where the chiasma and optic stalks were supposed to be rigidly determined. In the past some misunderstanding has been caused by confusion as to the exact meaning of the term 'chiasma.' In early stages the optic stalks are connected across the midline by a strip of tissue, very slender anteroposteriorly and very narrow transversely, lying in the depths of the primitive optic furrow. This may possibly best be referred to as the primitive chiasma. The definitive chiasma is formed later out of and in front of it when the optic nerve fibers invade the terminal ridge of the neural plate. In cyclopia in the absence of optic stalks neither the primitive nor definitive chiasma is formed. Throughout this discussion, 'chiasma' should be interpreted as referring to the primitive chiasma.

Corroborative evidence as to the distribution of the eye-forming potencies of the neural plate and the labile character of the



FIGS. 24-26. RESULTS OF THE HETEROTOPIC TRANSPLANTATION OF A MEDIAN STRIP OF THE NEURAL PLATE WITHOUT THE UNDERLYING ROOF OF THE ARCHENTERON OF *AMBLYSTOMA PUNCTATUM*

Figure 24, camera lucida drawing of donor. Figure 25-26, photographs of two sections through the brain and single eye which have differentiated from the transplant in the belly wall of the host. B, implanted brain, T., pigment layer of same. (Adelmann, '30).

FIGS. 27-28. RESULTS OF THE HETEROTOPIC TRANSPLANTATION OF A MEDIAN STRIP OF THE NEURAL PLATE TOGETHER WITH THE UNDERLYING ROOF OF THE ARCHENTERON OF *AMBLYSTOMA PUNCTATUM*

Figure 27, camera lucida drawing of donor. Figure 28, section through the brain and two bilaterally placed eyes which have developed from the transplant in the belly wall of the host. F.b., implanted forebrain, H, hypothalamus, L.oc., left eye of implant, R.oc., right eye of same (Adelmann, '30).

FIG. 29. MODEL (X CA. 30) OF AN *AMBLYSTOMA* EMBRYO IN THE NEURAL PLATE STAGE SHOWING THE RELATIONS OF THE ANTERIOR END OF THE ROOF OF THE ARCHENTERON TO THE NEURAL PLATE

The ectoderm has been removed on the left side. N., notochordal plate, Pm., mandibular portion of prechordal mesoderm, Pp., prechordal plate. (Adelmann, '32)

localization of its potencies has recently been gathered by Alderman ('35) for an Anuran. He finds that in *Hyla regilla* median rostral squares of anterior medullary plate transplanted to the belly wall of other individuals form single eyes attached to pieces of brain tissue and that the reversal of a median rostral square of medullary plate *without the substrate* results in the formation of brain tissue from presumptive eye and eye tissue from presumptive brain. "Eye determination, contrary to the conclusion of other workers is labile in the neural plate stage." Dragomirow ('32, '34) states that in *Triton taeniatus* the presumptive pigment and retinal layers of the eye are approximately equivalent in their potencies in early stages, the process of determination proceeding centrifugally from a central point corresponding approximately to the central portion of the pars optica. The retinal layer becomes specifically determined at about stage 29, but the pigment layer remains labile for a longer period.

The situation appears to be similar in the chick where Clarke ('34) finds that: (1) eye-forming capacity is present in a band across the blastoderm at the level of the node in streak stages and the anterior end of the notochord in head process stages, (2) there is a medio-lateral gradient in frequency of eye production and in capacity for differentiation, and (3) median strips of less than 84 micra, and therefore relatively few cells in width, from the brain floor of embryos up to the six-somite stage still gave pigmented and sensory layers of the retina. As further evidence, not conclusive in itself but significant in the light of the foregoing, the following findings may be briefly cited. (1) The fact that in "all experiments and in all species of amphibia investigated, fragments of a certain order of size of the eye anlagen of the neural plate and primary eye vesicle are capable of forming a

harmonic eye." (2) The fact that the fusion of two primary optic vesicles may form a single eye. (3) The fact that the site of the choroid fissure is not definitely determined in the primary optic vesicle. (4) The fact that atypical differentiation of the optic vesicle into two retinal cups may occur under certain conditions. (5) The fact that the urodelan eye possesses phenomenal regulative and restitutive powers throughout life. The above facts are cited from Mangold ('31) to whom the reader must be referred for references to the literature.

#### *Factors Responsible for Bilaterality of Eyes*

If then eye-forming materials as late as the early neural plate constitute a harmonious equipotential system with the potencies more intensely active medially than laterally, the question may be legitimately asked—what are the factors responsible for the normal differentiation of two eyes instead of but a single one? In other words what are the factors responsible for the attainment of the normal bilaterality of the eyes? In view of the profound effect which the roof of the archenteron (entomesoderm, substrate) has been observed to exert on the determination of the nervous system, we naturally look to it for factors possibly influencing the establishment of two centers of eye differentiation.

In order to determine the effect of the substrate upon the differentiation of the eye-forming region of the early neural plate, Adelmann ('30) excised median and left lateral strips of the anterior end of the early neural plate of the same donor and implanted them together with the underlying entomesoderm (substrate) into the belly wall of an older host. At the time of the operation the prechordal portion of the substrate consists of a narrow median strip, one cell layer thick, the prechordal plate, which is at this time still imbedded

in the roof of the archenteron and which extends from the anterior end of the notochordal plate to the cephalic extremity of the archenteron (fig. 29). The prechordal plate is flanked on each side by strips of prechordal mesoderm which are continued forward from the paraxial mesoderm lying on each side of the notochord. The strips of prechordal mesoderm which flank the prechordal plate later form the mesodermal cores of the mandibular arches from which the muscular elements of the arches are finally differentiated. For this reason it is convenient to refer to these as the mandibular portions of the prechordal mesoderm. At the time of operation the substrate thus exhibits a bilateral disposition of its parts occasioned by the characteristic arrangement of the median prechordal plate and the flanking mandibular portions of the prechordal mesoderm. There is however a potential continuity of mesoderm across the midline in the prechordal region for the prechordal plate is later separated from the roof of the archenteron in a caudo-cephalic direction, whereupon it expands laterally and ultimately furnishes bilaterally disposed masses of mesoderm which come to lie predominately dorsal and caudal to the eye and furnish the material from which are formed at least some of the eye muscles and an undetermined amount of mesenchyme of the head, chiefly in the region lying dorsal and anterior to the mandibular arch.

In the removal of the strips of medullary plate above described, the prechordal plate and very slender adjacent strips of the mandibular portions of the prechordal mesoderm were removed and implanted with the median strips of medullary plate, while the more lateral portions of the entomesoderm were removed and implanted with the lateral strips. Fifty-four per cent of the lateral strips transplanted

with substrate formed eyes as contrasted with eleven per cent when transplanted without. The substrate evidently reinforces the eye-forming potencies of the lateral regions of the neural plate.

Seventy-two per cent of the median strips transplanted with substrate formed eyes as contrasted with seventy per cent when transplanted without, not a very significant difference. While the median portion of the substrate in the early neural plate stage has little if any 'reinforcing' effect on the neural plate it possibly, even probably, did exert such an effect in early stages, judging from experiments of Spemann, Holtfreter and others.

The substrate does, however, have an interesting effect on the character of the eyes formed from the transplanted median strips. Two distinct eyes separated by ventral brain floor were formed in 47 per cent of the transplants of median strips with substrate, considering only those cases in which eyes were differentiated (figs. 27, 28). An additional 23 per cent formed two eyes, one of which was more or less rudimentary. No such cases were found in transplants of median strips without substrate, when, as previously noted, only single eyes were differentiated.

These results have recently been confirmed and extended for the anura by Alderman ('35) who finds that in *Hyla regilla* median rostral squares of medullary plate transplanted with substrate form paired eyes in seventy-five per cent of the transplants as contrasted with the single eyes formed from similar transplants without substrate. The possible deleterious effect of the separation of the substrate from the medullary plate is eliminated as a factor by the separation of the two before the medullary plate is implanted on top of the substrate. Paired eyes form from these transplants in about the same percentage of cases. Further, median rostral squares of medullary plate under-

bedded with median substrate taken from beneath more posterior regions of the plate do not form eyes. The 90° rotation of median rostral squares of substrate, having as their anterior boundary the inner rim of the transverse neural fold, disturbs the bilateral symmetry of the embryo to the extent that eye formation on the side receiving the eye-inducing substrate is in advance of eye formation on the side lacking it. The rotation of slightly more anterior median rostral pieces of substrate results in partial cyclopia.

The conclusion to be drawn from the experiments of Adelmann and Alderman is, first, that the substrate obviously has a profound effect on the induction of eye-forming potencies, a deduction which, of course, was already clear from experiments of Spemann and others. But they also indicate that as late as the early neural plate stage the eye-forming materials of the neural plate alone constitute a harmoniously equipotential system, plastic in its potentialities and capable of forming one or two eyes depending upon factors operating during development. While the eye-forming potencies of the neural plate alone are higher in the median region than laterally, the influence of the prechordal substrate is responsible for the establishment of two bilaterally situated centers of eye formation which arise as the material of the anterior portion of the neural plate expands. The conclusions of Adelmann are supported by Mangold ('31) who, in a striking experiment, produced typical cyclopia by excising the prechordal portion of the substrate in *Trison* (fig. 10).

#### *Abnormalities of the Substrate in Cyclopia*

In the light of the above, it is natural to speculate whether or not in experimentally induced cyclopia any structural peculiarities of the substrate are to be observed which might be indicative of an alteration of its normal influence upon the

neural plate. Adelmann ('29a, p. 276) some years ago called attention to the fact that the prechordal mesoderm is abnormally disposed in many cyclopean embryos. In a later study (Adelmann, '34) of a number of *Amblystoma* embryos rendered cyclopean by lithium treatment, an alteration of the normal bilateral disposition of the prechordal mesoderm was traced to the open medullary plate stage. Already at this time the prechordal mesoderm reveals a massive continuity across the midline with no indications of a division into a median prechordal plate and lateral mandibular portions such as are encountered in the normal embryo (cf. figs. 30, 31). In the notochordal region it was found that the characteristic arrangement of notochord and bilaterally disposed paraxial mesoderm was essentially normal except that the notochord was entirely separated out of the roof of the archenteron, even though the neural plate was widely open and the notochord had attained a degree of separation from the gut equal to that normally observed in embryos of 6-8 somites. The median continuity of the prechordal mesoderm was interpreted as due to a precocious separation of the prechordal plate mesoderm from the roof of the gut just as in the same sense the notochord had been precociously formed. This early continuity of the mesoderm across the midline is reflected later in the abnormal disposition of the muscle masses in the prechordal region with characteristic continuity across the midline (figs. 32, 33). The arrangement of muscle masses in the prechordal region of the older embryos examined agrees closely with that described or figured by a number of other authors (*Salamandra*: Korschelt and Fritsch, '10; Tsuda, '24; v. Querner, '25; *Rana*: LePlat, '19) and resembles the condition described by Wright and Wagner ('34) in otocephalic guinea-pigs.



Accompanying the abnormal disposition of the prechordal mesoderm, there were found all of the typical anomalies of the other organs of the head so characteristic

nervous tissue extending forward from the median optic aperture between the walls of the dorsal thalamus to the rostral end of the neural tube. The diencephalon and

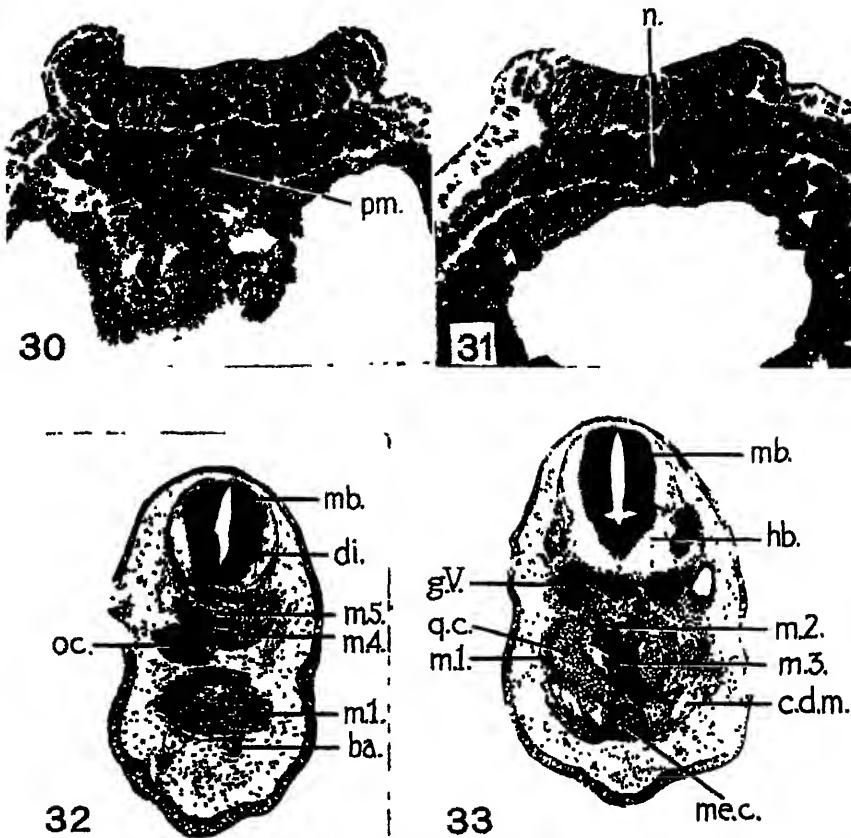


FIG. 30. A SECTION THROUGH THE PRECHORDAL REGION OF AN EMBRYO OF *AMBLYSTOMA PUNCTATUM* TREATED WITH LITHIUM CHLORIDE IN THE EARLY GASTRULA STAGE  
Note the massive continuity of mesoderm across the mid-line.

FIG. 31. A SECTION THROUGH THE NOTOCHORD OF THE SAME

The closure of the neural folds has been delayed but the separation of the notochord from the roof of the archenteron has proceeded to a degree equal to that encountered in normal embryos of 6-8 somites.

FIGS. 32-33. TWO SECTIONS (ARRANGED IN CEPHALO-CAUDAL SEQUENCE) BACK OF THE EYE OF A 12 MM. EMBRYO EXHIBITING CYCLOPIA PERFECTA

Note the continuity of the muscle masses across the mid-line in the mandibular region. *ba.*, balancer; *c.d.m.*, cephalo-dorso-mandibularis muscle; *di.*, diencephalon; *g.V.*, ganglion of the V nerve; *h.b.*, hindbrain; *m.1-5*, muscle masses derived from prechordal mesoderm; *mb.*, midbrain; *m.c.*, Meckel's cartilage; *oc.*, 'shaved' portion of the eye; *q.c.*, quadrate cartilage. (Adelmann, '34).

of cyclopia. Aside from the median eye, the most striking feature was the suppression of the normal bilaterality of the telencephalon, which in extreme cases was represented by only a median strip of

the midbrain to a lesser degree were abnormal. The prechordal portion of the pharynx was abnormal, ending blindly a short distance anterior to the notochord with the consequent absence of the oral

cavity and mouth. The transition to more normal conditions in the differentiation of the prechordal mesoderm was paralleled by more normal conditions in the brain, eye, and olfactory organ.

It was concluded that the correlation between abnormal features of the prechordal substrate and the prechordal regions of the brain supports the idea that the *typical* bilateral differentiation of the forebrain and eye, in particular, normally proceeds under the influence of the prechordal portion of the organizer or 'inducer,' and that cyclopia arising in the period of so-called 'labile determination' is probably due in most cases to alteration of the normal influence of the prechordal portion of the organizer.

Cotronei ('22) had previously noted that in lithium cyclops of *Rana*, the disturbance is primarily localized in the prechordal region, but concluded that lithium acted primarily upon the prechordal portion of the brain which in turn dominated the abnormal differentiation of the prechordal portion of the head. While it is possible that the nervous tissues may be inhibited and that this in turn may exert an influence upon the substrate (cf. Holtfreter, '33a, '33d), the weight of evidence seems to indicate that the suppression of the substrate, in many cases at least, may be the more important factor.

Lehmann ('33) from a less detailed study of chemically produced cyclopean urodeles comes to conclusions similar to Alderman's. The previously mentioned experiment of Mangold ('31) may also be cited as additional corroboration. Furthermore Raven ('33) describes a case of cyclopia which arose after early implantation of neural crest material which resulted in forcing the substrate away from direct contact with the eye-forming region. Alderman's ('35) experiment in which the rotation of median rostral

pieces of substrate results in partial cyclopia may be cited as further evidence pointing in the same direction.

#### *Influence of Substrate on More Caudal Parts of Nervous System*

While the exact nature of the influence of the substrate is not yet clear, Holtfreter ('34) reports what appears to be an essentially comparable phenomenon in the differentiation of more caudal portions of the nervous system under various conditions. He states that

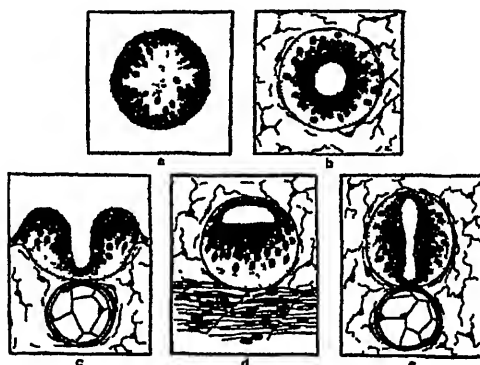
the influence of inductors upon the reacting material is exerted mostly in two directions for which medullary induction may serve as an example. It acts in the first place to determine the material: the ectoderm becomes nerve cells . . . and in the second case it acts as a determiner of form. In order that organ-formation may pursue a normal course, a connective tissue substrate is necessary. This may be explained by a schema (fig. 34) constructed on the basis of many observations. If a piece of medullary tissue which has already been underlain by the substrate and is therefore determined is isolated, it develops further into nervous tissue when floating free (in the medium). Lacking a substrate and modelling influences in its neighborhood it usually rounds up into a sphere, on the periphery of which ganglion nuclei lie, while the nerve fibers course centrally (fig. 34a). If the nervous tissue develops within a mesenchymal mantle, a vesicle or tube with a central lumen is usually formed. The fibers here run centrifugally . . . (fig. 34b). When the neural tube is induced by musculature alone, there always arises, when mesenchyme is present, a tube with an excentrically placed lumen. (fig. 34d) . . . If the medullary tissue is induced by a notochord, the lumen is elongated in slit-like fashion down to the base. If in addition the connective tissue mantle is lacking, the medullary mass remains groove-like (*asyntaxis medullaris*) and with respect to the distribution of its nuclei behaves like the explant (fig. 34c). But if neighboring tissue (*nachbar Gewebe*) is present all around it, the medullary mass closes to form a tube which resembles a cross section of the normal spinal cord.

Lehmann ('26) had previously shown the influence of the presence of the notochord on the bilateral massing of material of the neural tube.

The exact nature of the influence, whether chemical, mechanical or both, which has so marked an effect in determining the form of the induced nervous tissue is not clear, but it will be apparent that the influence of the substrate on the normal bilateral massing of the forebrain and eye is possibly of an order similar to that revealed by Holtfreter's experiments, and if so, a uniformity of behavior would exist throughout the central nervous system. It may even be suggested that the typical conformation of pre-

absence of the notochord and permitted the fusion of paraxial mesoderm under the neural tube. In this region the characteristic floor plate of the neural tube was lacking and the typical bilateral arrangement replaced by a basal massing of medullary material.

The rôle of the substrate (inducer) may consist, as Raven ('33) suggests, in serving in some way to "center" the organ anlagen which at first seem generally to be laid down with relatively diffuse boundaries. Raven cites two factors which



34

FIG. 34. SCHEMATIC REPRESENTATION OF THE FORMATIVE INFLUENCE OF DIFFERENT NEIGHBORING TISSUES UPON NERVOUS TISSUE

(a) Pure culture of nervous tissue. (b) Neural tube in the midst of mesenchyme. (c) Neural plate induced by notochord only; it remains open but possesses a characteristically thin floor. (d) Neural tube with excentric lumen resting upon muscle. (e) Normal neural tube resting upon notochord in the midst of neutral neighboring tissue. (From Holtfreter, '34).

chordal plate flanked laterally by the mandibular portions of the prechordal mesoderm may play essentially the same rôle in determining the typical bilateral massing of materials of the eye and the prechordal region of the brain that the characteristic arrangement of notochord flanked by the somites does in determining the characteristic bilateral massing of material in more caudal regions. In this connection an experiment of Lehmann's ('26) may be cited, in which the removal of the prospective notochord from an early gastrula resulted in the

must be distinguished (1) the formation of the anlage territory and (2) the delimitation of the materials for the organ which probably follows in most cases a centering of the "Organisationspotenz" in a narrowly circumscribed territory. Several possibilities exist: (1) The organ anlagen are laid down "centered" from the first under the influence of the organizer. (2) The organ anlagen are originally diffuse, with approximately uniform distribution of the "Organisationspotenz," the centering occurring autonomously without the coöperation of the organizer.

(3) As above, but the 'centering' occurs under the influence of the organizer. The last possibility seems best to fit the facts in the present instance, and seems also to fit in with Raven's studies on the inductive capacities of the neural crest.

#### *Influence of Neural Plate*

While there is thus experimental evidence that the normal substrate probably plays a large part in determining the typical bilateral symmetry of the neural tube and eye, an experiment of Mangold's ('32) indicates that its place may be more or less successfully taken by the neural plate acting as inducer. He reports the induction of a bilaterally symmetric brain with two eyes by the cephalic third of the right half of the neural plate. We have already noted that the neural plate may induce eye differentiation but the factors responsible for the induction of two bilaterally disposed eyes in this instance are no clearer than they are in the case of the normal substrate. Whether a regulation of the inducing tissues to a bilaterally symmetric structure has preceded the induction and thus influenced the bilateral massing of the induced tissue is not clear. Possibly the implanted medullary tissue furnished the proper mechanical support for the bilateral expansion of the eye-forming materials, a rôle which may also be played by the normal substrate in this connection.

At first it would appear that the induction of secondary embryos by dead organizers and the induction of typical bilaterally symmetric heads by lateral fragments of inducing substances were inimical to the validity of the facts stated above. Holtfreter ('33a), however, has recently shown that such is not the case and has furthermore shown that the materials of the marginal zone have remarkable regulative powers, lateral por-

tions exhibiting regulation and tending to become reconstituted as bilaterally symmetric wholes. Thus a piece of the lateral wing of the presumptive chorda when cultured in vitro differentiated a notochord, bilaterally disposed musculature and at its upper end nervous tissue and epidermis. In addition to bringing further evidence of the existence of regional differences in the action of the organizer in a longitudinal direction, previously adduced by Spemann, he states that the bilateral character of the induction in cases where bilateral heads are induced by lateral portions of the marginal zone

is conditioned by the fact that the implant itself is first bilaterally regulated and as such induces symmetrical brain structures. This very tendency of a partial organizer when transplanted to complete itself as a more or less integral whole, either from its own substance or by the incorporation of host material, is, indeed, the principal characteristic of the transplanted partial organizer. Thereby it will always be distinguished from a dead organizer. (Holtfreter, '33a, p. 428).

In this connection, however, it must be clearly understood that while the cyclopean head is characterized by an atypical bilaterality or massing of its parts, it is, nevertheless, bilaterally symmetric.

#### *Induction of Cyclopia by Abnormalities of Substrate*

The facts drawn from various quarters then seem to favor the view that cyclopia may in many cases owe its genesis to an alteration of the influences normally exerted by the prechordal portion of the substrate upon the normal bilateral massing of the tissue of the eyes and prechordal region of the brain. In this light furthermore, we find a simple explanation of many facts heretofore difficult to explain. Thus, the results of Spemann's ('01-'03) constriction experiments are probably due to the fact that the pre-

chordal region of the inductor was subdivided, resulting in the formation of two heads. Whether cyclopia results or not would depend upon the degree to which the inducing material is able to regulate. His reversal experiments also find a simple explanation, the reversal of the substrate together with the medullary material being responsible for the result. As previously noted, Alderman ('35) finds that reversal of a segment of the early neural plate without substrate results in the formation of eye from presumptive brain and vice versa.

This explanation is also in harmony with the results obtained in the production of cyclopia by the alteration of various environmental factors. It is a well known fact (Bellamy, '19, '22; Woerdeman, '33) that the dorsal lip of the early blastopore where the prechordal region of the organizer is situated before invagination, is the site of intense metabolic activity. Since, as the evidence seems to indicate (Child, '28; Stockard, '21), adverse environmental influences act most vigorously upon whatever regions happen to be metabolizing most actively at the time of their action, and since cyclopia is produced only when embryos are adversely affected by chemicals or otherwise in the early stages of gastrulation when the prechordal portion of the organizer is not yet invaginated, the chances of its being adversely affected would be great. The work of Adelmann and Lehmann shows that a deleterious effect upon the substrate, as reflected in its abnormal differentiation, may actually be demonstrated in cyclopia, in which case, however, its eye inducing ("material bestimmend," Holtfreter) powers have not been destroyed but its form-determining ("formbestimmend," Holtfreter) influences have been impaired. In case the action of the inhibiting agent has been so severe as to destroy entirely the

eye-inducing properties of the substrate, anophthalmia would be the expected result.

It has been noted that in cyclopia the typical bilaterality of the parachordal region of the body has not been disturbed by the action of lithium in contrast to the rather striking suppression of bilaterality in the prechordal region. The explanation is possibly to be found in the fact that a potential continuity of mesoderm across the midline exists in the prechordal region, since the prechordal plate, itself prospectively mesoderm, forms a median area of prospective continuity between the more laterally situated mesoderm. In prospectively more caudal regions, however, the mesoderm is separated medially by the notochordal plate and it seems logical to assume that in the latter region there exists a more strongly impressed inherent bilaterality than in the prechordal region.

#### *Cyclopia without Abnormalities of Substrate*

It would be rash to assume, however, that the action of adverse environmental factors is always exerted on the entomesoderm (substrate) alone. Stockard ('09b), LePlat ('19), Cotronei ('22), Wright and Wagner ('34) among others, assume that the action of adverse environmental factors is exerted entirely on the medullary plate. In the final analysis, the form and relations of the cyclopean eye and brain are an expression of abnormal developmental behavior on the part of the anterior end of the neural plate and tube. The normal bilateral growth, expansion and differentiation of the latter appear normally to be related to influences arising from the normal organismic environment of the medullary plate (in particular the dorsal lip of the early blastopore or the anterior end of the roof of the archenteron); its failure to occur appears in many

cases to be related to abnormal influences arising within the organism. It is, therefore, logical to infer that abnormal conditions prevailing in the external milieu, by acting directly upon the neural plate may produce essentially the same result.

It should, of course, be clearly kept in mind that, as Mangold ('31) points out, the end result is a product of the reaction of two materials, the substrate and the neural plate, which may be affected separately or in combination (See also Lehmann, '34). It is, indeed, likely that the neural plate may itself be so adversely affected that it is unable to respond typically to formative influences arising from the normal substrate, and we may occasionally expect to find cyclopia or even anophthalmia arising in conjunction with more or less normal differentiation of the substrate. But, on the other hand, normal differentiation of the substrate does not necessarily mean that it has exerted its normal influence on the material and morphological differentiation of the nervous system. Again, the neural plate may be able to overcome to some degree abnormal influences exerted by the substrate. This would naturally depend upon the degree of determination attained by the neural plate and its subdivisions and would probably vary in different species. Consequently normal or almost normal development of the eyes may be expected to be found in some forms although the development of parts derived from the substrate is more or less atypical. Otocephaly, for instance, need not necessarily be accompanied by cyclopia. It is possible, however, that the suppression of the jaws and mouth in these cases may have occurred after the eye-forming material had been determined.

Cotronei ('22) who accepts a rigid determination of the eyes in the neural plate believes that lithium and other

similar environmental agents affect the prechordal region of the neural plate primarily and inhibit its normal expansion and growth. He also assumes that the prechordal neural plate directs the differentiation of the rest of the head and results in the establishment of the other cranial anomalies of cyclopia. The lack of expansion of the prechordal brain results in the fusion of the two rigidly determined eye-forming areas because of lack of space to expand. There is undoubtedly some truth in his contention. Before the appearance of the dorsal lip of the blastopore in amphibia an area of heightened metabolic activity in the region of the animal pole, in the region of the presumptive neural plate has been demonstrated by Bellamy ('19), and Holtfreter ('33d) has shown that the induced material in turn reacts upon its substrate. Further, it is undoubtedly true that to a large extent the characteristic pattern of growth and expansion of the prechordal brain determine in large part the pattern of the head (see Kingsbury and Adelman, '24), but it is still uncertain to what extent these are secondary factors normally set in action initially by the substrate. Guareschi ('34) has recently attempted to substantiate the interpretation of Cotronei by a combination of the use of vital dyes and the action of lithium. After staining median and lateral areas of the prospective eye-forming region, the eggs were treated with lithium solutions and cyclopia induced. The stained eyes were then studied in the gross specimens and it appeared that the cyclopean eye was always stained the color of the lateral areas of the neural plate. He concludes that the two eyes have fused by displacing median material. However, before his interpretation can be accepted, the work will have to be repeated by the study of the dye in sections. His figure 32,

furthermore, clearly shows a blue median strip in the cyclopean eye derived from the stained median area of the gastrula.

#### *Other Abnormal Features of the Cyclopean Head*

For the moment the possibility that an inhibition of the normal reactions of the medullary tissue may in some cases be the initiating factor may be set aside in favor of that possibility which seems better to fit the majority of cases, namely an early inhibition of the prechordal region of the substrate. On this basis we may proceed to examine some of the other typical abnormal features of the cyclopean head. This assumption, for instance helps to explain the frequent association with cyclopia of anomalies of the jaws (otocephaly) and mouth; an inhibition of the prechordal substrate as expressed in a suppression of its bilaterality accounting for the fusion of the muscle masses in the mandibular region. Wright and Wagner ('34) in their study of otocephalic guinea-pigs, many of which were cyclopean, believed that all of the abnormalities which they encountered could be traced to a small number of centers—in usual but not invariable order of frequency of defect—ventral mandibular arch, fronto-nasal process, olfactory placodes and cerebral vesicles, median optic rudiment, progressively posterior parts of the brain, dorsal portion of the mandibular arch and hyoid arch. They advance the hypothesis that the basic factor in this class of abnormalities is inhibition of the anterior medullary plate and associated ectodermal placodes, and that one of the effects of such inhibition is interference with the formation and migration of the neural crest. To the failure of the neural crest to migrate they attribute the abnormal formation of the skeletal elements of the jaw and to this in turn the abnormal disposition of the muscles. However, in the cyclopean uro-

deles of Adelmann and Lehmann, atypical features of the prechordal substrate were detected before the neural crest normally migrates and it would seem more likely that the abnormal disposition of the prechordal mesoderm had determined the abnormal conformation of the derivatives of the neural crest. From the order of frequency noted by Wright and Wagner ('34) it would appear that the prechordal mesoderm was more vulnerable than the neural plate. However, it must be kept in mind that a relatively late suppression of the mandibular arches would result in otocephaly as will be apparent from the figures of Streeter ('22) and in this case cyclopia would not be expected to accompany it.

The median massing of the prechordal mesoderm in *Amblystoma* seems to effectively prevent contact between the pharynx and the presumptive oral ectoderm, thus accounting for the absence of the oral cavity in many cases. We know from the work of Adams ('24) and Ströer ('33) that the oral ectoderm depends upon contact with the pharynx for its normal differentiation.

Adelmann ('34) found further that the arrangement of the prechordal mesoderm in cyclopia often prevents contact between the brain floor and ectoderm in the hypophyseal region, which in connection with Blount's ('32) finding that the differentiation of the anterior lobe of the hypophysis depends upon contact between brain and ectoderm seems to explain the absence of the anterior lobe of the hypophysis in many cases.

The singleness or doubleness of the olfactory sac of cyclopean *Amblystoma* embryos was found to be correlated with the degree of typical bilateral differentiation attained by the prosencephalon, and it appears likely that inductive activity on the part of the latter is responsible for

the result. Raven ('33) reports a case in which supernumerary olfactory organs were apparently induced by splitting of the anterior end of the brain. In cyclopia perfecta, due to the suppression of the typical bilaterality of the forebrain, but one olfactory placode is induced.

In adopting this approach, however, we must not be deluded into imagining that the problem of the harmonic development of the cyclopean head is a simple one. While at present it would appear that the end result is largely determined by the balance struck between the reacting material of the neural plate and ectoderm and the inducing material of the substrate which may, as we have supposed, be affected separately or in combination, the final picture is, however, no doubt influenced by a complex of factors not yet clearly identified. In its normal development the head exhibits what may be designated, for want of a better term, a certain 'wholeness' or unity, comparable to that exhibited by the organism as a whole. It is achieved by and is an expression of a delicate balance between the various parts of which it is composed and correlative adjustment in the development of the subordinate parts which in turn make up larger units. Thus Dragomirow ('33) describes a coördination of 'partial processes' operating within the eye itself and no doubt a similar situation exists in the case of the other organs of the head. The harmonious development of the normal head is thus brought about by the harmonious coöperation of a number of factors most of which are still obscure. The harmonic development of the cyclopean head will only be completely understood when the nature of some of these more obscure processes is better known.

#### V. SUMMARY

From the foregoing we see that the controversy as to whether the "eye enlage

is primarily median and single or not" has largely lost its point and becomes in part a matter of definition. Under the influence of the roof of the archenteron there is probably at first established a diffusely localized, homogeneous or harmoniously equipotential 'eye-field.' On this the substrate normally acts further to establish two bilaterally situated centers of eye-formation. But as late as the early neural plate stage, in amphibia at least, they are not rigidly determined and the eye-forming materials of the gastrula and of the early neural plate should be regarded as potentially either single or double, the outcome depending upon factors operating during development.

Finally, in order that a clearer differentiation can be made between "Observation and Reflection" than has been possible in the preceding pages, it may be wise to state what seem now to be the established facts.

(1) The localization of eye-forming potencies in the appropriate region of the anterior end of the neural plate normally occurs under the influence of the roof of the archenteron (Spemann, '31; Mangold, '28; Holtfreter, '33a, '34; *et al.*).

(2) The substrate (entomesoderm) determines not only the differentiation of the ectoderm as nervous tissue but also its morphology (Holtfreter, '34).

(3) The presumptive or prospective eye anlage, comprising the materials for both eyes, occupies a median territory of the anterior neural plate measuring but  $\frac{1}{3}$ — $\frac{1}{4}$  of the greatest diameter of the plate. The materials for the eyes are separated antero-medially by material whose presumptive significance is to form a part of the lamina terminalis and connected (or separated?) posteriorly by a narrow zone of material normally involved in the formation of the primitive chiasma (Manchot, '29; Woerdeman, '29).

(4) The eye-forming potentialities of



the anterior end of the neural plate are diffusely localized (Adelmann, '29; Mangold, '31) and so far as the neural plate alone is concerned are harmoniously equipotential, any portion being able to form any part of the optico-ocular apparatus (Adelmann, '30).

(5) Eye-forming potencies are higher medially than laterally (Adelmann, '30; Clarke, '34).

(6) The bilateral differentiation of two eyes from the relatively plastic eye-forming materials of the neural plate normally depends upon influences exerted by the underlying entomesoderm (Adelmann, '30; Holtfreter, '33a; Alderman, '35).

(7) In cyclopia atypical differentiation of the prechordal substrate often occurs,

the degree to which the substrate is abnormally disposed is correlated in particular with corresponding degrees of abnormality of the brain and eyes (Lehmann, '33; Adelman, '34).

(8) Cyclopia may be produced by excision of the prechordal portion of the roof of the archenteron (Mangold, '31).

In the light of the foregoing, we have attempted in the preceding pages not to 'explain everything' in connection with cyclopia for we realize that the situation is complex and that the problem is far from solved, but to present consistently a line of thought or point of view which we think is interesting and suggestive, and which we hope will be stimulating.

#### LITERATURE CITED

- ADAMS, A. E. 1924. An experimental study of the development of the mouth in the amphibian embryo. *Jour. Exp. Zool.*, vol. 40, pp. 311-379.
- ADELMANN, H. B. 1929a. Experimental studies on the development of the eye. I. The effect of the removal of median and lateral areas of the anterior end of the urodean neural plate on the development of the eyes. *Jour. Exp. Zool.*, vol. 54, pp. 249-290.
- . 1929b. Experimental studies on the development of the eye. II. The eye-forming potencies of the median portions of the urodean neural plate. *Jour. Exp. Zool.*, vol. 54, pp. 291-317.
- . 1930. Experimental studies on the development of the eye. III. The effect of the substrate ('Unterlagerung') on the heterotopic development of median and lateral strips of the anterior end of the neural plate of *Amblystoma*. *Jour. Exp. Zool.*, vol. 57, pp. 223-281.
- . 1932. The development of the prechordal plate and mesoderm of *Amblystoma punctatum*. *Jour. Morph.*, vol. 54, pp. 1-67.
- . 1934. A study of cyclopia in *Amblystoma punctatum* with special reference to the mesoderm. *Jour. Exp. Zool.*, vol. 67, pp. 217-281.
- ALDERMAN, A. L. 1935. The determination of the eye in the anuran, *Hyla regilla*. *Jour. Exp. Zool.*, vol. 70, pp. 205-232.
- ALLAN, R. 1848. Dissection of a human astomatous cyclops. *Lancet*, pp. 227-8.
- ANASTASI, O. 1913. Sul comportamento di alcuni innesti di occhi nelle larve di *Discoglossus pictus*. *Arch. Entomol.*, Bd. 37, S. 222-232.
- VON BAER, K. E. 1828. Ueber Entwicklungsgeschichte der Thiere. *Königsberg*.
- BALLANTYNE, J. W. 1904. Manual of Antenatal Pathology and Hygiene. II. The Embryo. *Edinburgh*.
- BAUTZMANN, H. 1926. Experimentelle Untersuchungen zur Abgrenzung des Organisationszentrums bei *Triton taeniatus*. *Arch. f. Entomol.*, Bd. 108, S. 283-321.
- . 1929. Über bedeutungs fremde Selbstdifferenzierung aus Teilstücken des Amphibienkeimes. *Naturwiss.*, Bd. 17, S. 818-827.
- BELLAMY, A. W. 1919. Differential susceptibility as a basis for modification and control of early development in the frog. *Biol. Bull.*, vol. 37, pp. 312-361.
- . 1922. Differential susceptibility as a basis for modification and control of early development in the frog. *Am. Jour. Anat.*, vol. 30, pp. 473-502.
- BLANC, L. 1895. Sur l'otocéphalie et la cyclopie. *Jour. de l'Anat. et de la Phys.*, T. 31, pp. 187-288.
- BLOUNT, R. F. 1932. Transplantation and extirpation of the pituitary rudiment and the effects upon pigmentation in the urodele embryo. *Jour. Exp. Zool.*, vol. 63, pp. 113-141.
- BOCK, E. 1889. Beschreibung eines atypischen Cyclops. *Klin. Monatsbl. f. Augenheilk.*, Bd. 27, S. 508-522.

- BORN, G. 1897. Ueber Verwachsungsversuche mit Amphibienlarven. *Arch. f. Entmisch.*, Bd. 4, S. 439-465; 517-623.
- CHIDESTER, F. E. 1914. Cyclopia in mammals. *Anat. Rec.*, vol. 8, pp. 355-366.
- CHILD, C. M. 1920. Some considerations concerning the nature and origin of physiological gradients. *Biol. Bull.*, vol. 39, pp. 147-187.
- . 1921. The Origin and Development of the Nervous System. Univ. of Chicago Press, Chicago, Ill.
- . 1928. The physiological gradients. *Protoplasma*, Bd. 5, S. 447-476.
- CLARK, L. F. 1934. Regional differences in eye-forming capacities of early chick blastoderms as studied in chorio-allantoic grafts. *Anat. Rec.*, vol. 58, suppl., pp. 54-55.
- COTRONI, G. 1922a. Corrélation et différenciations. Essai de morphologie causale sur la tête des Amphibiens. *Arch. Ital. de Biol.*, T. 71, pp. 1-29.
- . 1922b. Suscettibilità differenziale gradiente assiale e rapporti tra correlazioni e differenziazione. *Rend. R. Accad. Lincei, Cl. Sci. fis., mat. e nat.*, vol. 31, ser. 5a, pp. 473-476.
- DALTROP, A. 1932. Über die gegenseitige Vertretbarkeit verschiedener Abschnitte der Hirnanlage in der Medullarplatte von Amphibien. *Arch. f. Entmisch.*, Bd. 127, S. 1-60.
- DARBYSH, C. 1877. Recherches sur la Production Artificielle des Monstrosités ou Essais de Tératogénie Expérimentale. Paris, 1877. 2me Ed., Paris, 1891.
- . 1891. Mode de formation de la cyclopie. *Ann. d'ocul.*, T. 106, pp. 171-182.
- DETWILER, S. R. 1929. Some observations upon grafted eyes of frog larvae. *Arch. f. Entmisch.*, Bd. 116, S. 555-566.
- DRAGOMIROV, N. 1932. Über Entwicklung von Augenbechern aus transplantierten Stückchen des embryonalen Tapetums. *Arch. f. Entmisch.*, Bd. 126, S. 636-637.
- . 1933. Über Koordination der Teilprozesse in der embryonalen Morphogenese des Augenbechers. *Arch. f. Entmisch.*, Bd. 129, S. 522-560.
- . 1934. Über die Determination der Augenbecherblätter bei *Triton taeniatus*. *Arch. f. Entmisch.*, Bd. 131, S. 540-542.
- VAN DUYSE, G. 1909. Cyclopie avec cryptophthalmos et kystes colobomateux. *Arch. d'ophth.*, T. 29, pp. 65-77.
- FÉLIX, CH. 1899. Influence du repos sur les effets de l'exposition préalable aux vapeurs d'alcool avant l'incubation de l'œuf de poule. *Compt. Rend. Soc. Biol.*, pp. 255-258.
- . 1900. Note sur l'influence de l'échauffement préalable sur l'incubation de l'œuf de poule. *Compt. Rend. Soc. Biol.*, pp. 796-797.
- FISCHER, A. 1921. Über normale und abnorme Entwicklung des Auges. I. Über Art und Ort der ersten Augenanlage sowie über die formale und kausale Genese der Cyclopie. II. Zur Entwicklungsmechanik der Linse. *Arch. f. Entmisch.*, Bd. 49, S. 383-462.
- GEMMILL, J. F. 1906. On cyclopia in osseous fishes. *Proc. Zool. Soc. London*, 1906, I., pp. 443-449.
- GROFFROY-ST. HILAIRE, E. 1826. Sur les Déviations organiques provoquées et observées dans un établissement d'incubation artificielle. *Mém. Mus. d'Hist. nat., Paris*, T. 13, pp. 289-296.
- GROFFROY-ST. HILAIRE, I. 1832-1837. Histoire générale et particulière des Anomalies de l'Organisation chez l'Homme et les Animaux. Bruxelles.
- GOODALE, H. D. 1911. The early development of *Spelerpes bilineatus* (Green). *Am. Jour. Anat.*, vol. 12, pp. 173-247.
- GUARACHI, C. 1934. Metodo combinato della suscettibilità differenziale e dei colori vitali per lo studio embrionale degli anfibii. *Reale Accad. d'Ital., Mem. Cl. Sci. Fis., mat. e nat.*, T. 5, pp. 209-237.
- HANNOVER, A. 1882. Den menneskelige Hjerneskals Bygning ved Cyclopia. Copenhagen.
- HARRISON, R. G. 1933. Some difficulties of the determination problem. *Am. Naturalist*, vol. 68, pp. 306-321.
- VON HIEFEL, E. 1900. Die Missbildungen und angeborenen Fehler des Auges. Graefe-Sacmisch Handb. d. Augenheilk., 2nd. Ed. Bd. 2.
- HOADLEY, L. 1926. Developmental potencies of parts of the early blastoderm of the chick. I. The first appearance of the eye. *Jour. Exp. Zool.*, vol. 43, pp. 151-178.
- . 1928. On the localization of developmental potencies in the embryo of *Fundulus heteroclitus*. *Jour. Exp. Zool.*, vol. 52, pp. 7-44.
- HOLTGRETER, J. 1929. Über die Aufzucht isolierter Teile des Amphibienkeimes. I. Methode einer Gewebezüchtung in vivo. *Arch. f. Entmisch.*, Bd. 117, S. 421-510.
- . 1933a. Organisationsstufen nach regionaler Kombination von Entomesoderm mit Ektoderm. *Biol. Zentralbl.*, Bd. 53, S. 404-431.
- . 1933c. Einige menschliche Missbildungen im Lichte neuerer Amphibiensexperimente. *Sitzungsber. Ges. f. Morph. und Phys., München*, Jahrg. 42, S. 1-15.
- . 1933d. Die totale Exogastrulation, eine Selbstablösung des Ektoderms vom Entomesoderm. *Arch. f. Entmisch.*, Bd. 129, S. 669-793.

- . 1934. Formative Reize in der Embryonalentwicklung der Amphibien, dargestellt an Explanationsversuchen. *Arch. f. exp. Zellf.*, Bd. 15, S. 281-301.
- HUCHKE, E. 1832. Über die erste Entwicklung des Auges und die damit zusammenhängende Cyclopie. *Mackels Arch. f. Anat. u. Phys.*, S. 1-47.
- JOSEPHY, H. 1913. Otocephalie und Trioccephalie. In—Schwalbe: Die Morphologie der Missbildungen, III. Teil, I. Abt., S. 247-270.
- KRIEGL, F. 1928. Beiträge zur Anatomie, zur Entwicklungsgeschichte und zur Stammesgeschichte der Schorgane der Cyclostomen. *Zeitsch. mikrosk.-anat. Forsch.*, Bd. 12, S. 391-456.
- KELLYCOTT, W. E. 1916. The effects of low temperature upon the development of *Fundulus*. *Am. Jour. Anat.*, vol. 20, pp. 459-482.
- KING, H. D. 1905. Experimental studies on the eye of the frog embryo. *Arch. f. Entom.*, Bd. 19.
- KINGSBURY, B. F., and H. B. ADLERMAN. 1924. The morphological plan of the head. *Quart. Jour. Mic. Sci.*, vol. 68, pp. 239-285.
- KLOPFER, A. 1921. Familiäres Vorkommen von Cyclopie und Arrhinencephalie. *Monatsschr. f. Geburtsk. u. Gynaek.*, Bd. 56, S. 59-71.
- KORSCHKE, E., and C. FERTSCH. 1910. Über eine Missbildung der Larve von *Salamandra maculata*. *Arch. Entom.*, Bd. 30, II. Teil, S. 291-317.
- KUNDRAT, H. 1882. Arrhinencephalie als typische Art von Missbildung. *Grax*, 1882.
- VON KUPFER, C. 1890. Die Entwicklung von *Psittomyxus planeri*. *Arch. f. mik. Anat.*, Bd. 35, S. 469-485.
- KUSCH, W. 1929. Interplantation umschriebener Zellbezirke aus der Blastula und der Gastrula von Amphibien. I. Versuche an Urodelen. *Arch. f. Entom.*, Bd. 120, S. 192-271.
- LEHMANN, F. E. 1926. Entwicklungsstörungen in der Medullaranlage von *Triton*, erzeugt durch Unterlagerungsdefekte. *Arch. f. Entom.*, Bd. 108, S. 243-282.
- . 1928. Die Bedeutung der Unterlagerung für die Entwicklung der Medullarplatte von *Triton*. *Arch. f. Entom.*, Bd. 113, S. 123-171.
- . 1933. Die Augen- und Linsenbildung von Amphibien-embryonen unter dem Einfluss chemischer Mittel. *Rev. Suisse Zool.*, T. 40, pp. 251-264.
- . 1934. Die Linsenbildung von *Rana fusca* in ihrer Abhängigkeit von chemischen Einflüssen. *Arch. f. Entom.*, Bd. 131, S. 333-361.
- LEPLAT, G. 1913. Production artificielle de tétards cyclopes et anophtalmes. *Ann. Soc. de Méd. de Gand*, n.s., T. 4, pp. 230-239. *Belgique méd.*, Gand, T. 20, pp. 279-283.
- . 1914. Localisation des premières ébauches oculaires chez les vertébrés. Pathogénie de la cyclopie. *Anat. Anz.*, Bd. 46, S. 280-289.
- . 1919. Action du milieu sur le développement des larves d'amphibiens. Localisation et différenciation des premières ébauches oculaires chez les vertébrés. Cyclopie et Anophtalmie. *Arch. de Biol.*, T. 30, pp. 231-321.
- LEWIS, W. H. 1907. Experiments on the origin and differentiation of the optic vesicle in Amphibia. *Am. Jour. Anat.*, vol. 7, pp. 259-277.
- . 1909. The experimental production of cycloopia in the fish embryo (*Fundulus heteroclitus*). *Anat. Rec.*, vol. 3, pp. 175-181.
- . 1910. Localization and regeneration in the neural plate of amphibian embryos. *Anat. Rec.*, vol. 4, pp. 191-198.
- LICHTUS, F. 1634. De Monstrorum Natura, Causis et Differentiis. *Patauij*, P. Frambottus.
- LOEB, J. 1915. The blindness of the cave fauna and the artificial production of blind fish embryos by heterogeneous hybridization and by low temperatures. *Biol. Bull.*, vol. 29, pp. 50-67.
- MCCLENDON, J. F. 1912a. An attempt toward the physical chemistry of the production of one-eyed monstrosities. *Amer. Jour. Phys.*, vol. 29, pp. 289-297.
- . 1912b. The effects of alkaloids on the development of fish (*Fundulus*) eggs. *Amer. Jour. Phys.*, vol. 31, pp. 131-140.
- MALL, F. P. 1908. A study of the causes underlying the origin of human monsters. *Jour. Morph.*, vol. 19, pp. 3-368.
- . 1917. Cycloopia in the human embryo. *Contributions to Embryology*, no. 15, *Carnegie Inst. Wash.*, Pub. no. 226, pp. 5-33.
- MANCHOT, E. 1929. Abgrenzung des Augenmaterials und anderer Teilbezirke in der Medullarplatte; die Teilbewegungen während der Auffaltung (Farbmarkierungsversuche an Keimen von Urodelen). *Arch. f. Entom.*, Bd. 116, S. 689-708.
- MANGOLD, O. 1923. Transplantationsversuche zur Frage der Spezifität und der Bildung der Keimblätter. *Arch. f. mik. Anat. u. Entw. mech.*, Bd. 100, S. 198-301.
- . 1928. Das Determinationsproblem. I. Das Nervensystem und die Sinnesorgane der Seitenlinie unter spezieller Berücksichtigung der Amphibien. *Ergeb. d. Biol.*, Bd. 3, S. 151-227.
- . 1929a. Die Induktionsfähigkeit der Medullarplatte und ihrer Bezirke. *Verh. Deutsch. Zool. Ges.*, 1929, S. 166-173.
- . 1929b. Experimente zur Analyse der Determination und Induktion der Medullarplatte. *Arch. f. Entom.*, Bd. 117, S. 586-696.

- . 1931. Das Determinationsproblem. III. Das Wirbeltierauge in der Entwicklung und Regeneration. *Ergeb. d. Biol.*, Bd. 7, S. 193-403.
- . 1932. Autonome und komplementäre Induktion bei Amphibien. *Naturwiss.*, Jahrg. 20, S. 371-375.
- . 1933. Über die Induktionsfähigkeit der verschiedenen Bezirke der Neurula von Urodelen. *Naturwiss.*, Jahrg. 21, S. 761-766.
- MANGOLD, O., and H. SPEMANN. 1927. Über Induktion von Medullarplatte durch Medullarplatte im jüngeren Keim; ein Beispiel homogenetischer oder assimilatorischer Induktion. *Arch. f. Entsch.*, Bd. 111, S. 341-421.
- MARX, A. 1925. Experimentelle Untersuchungen zur Frage der Determination der Medullarplatte. *Arch. f. Entsch.*, Bd. 105, S. 19-44.
- MECKEL, J. F. 1826. Ueber Verschmelzungsbildungen. *Arch. f. Anat. u. Phys.*, vol. 1, S. 238-315.
- NEEDHAM, J. 1931. *Chemical Embryology*. Cambridge.
- OGNEW, B.W. 1930. Die Zyklopie im Zusammenhang mit Anomalien anderer Organe. *Anat. Anz.*, Bd. 70, S. 241-245.
- PANTUM, P. 1860. Untersuchungen über die Entstehung der Missbildungen. *Berlin*.
- PAOLUCCI, L. 1874. Sopra una forma mostruosa della *Myliobatis noctula*. *Atti della società Italiana di Sc. Naturali*, T. 17, pp. 60-63.
- PASQUINI, P. 1927a. Ricerche di embriologia sperimentale sui trapianti omeoplastici della vescicola ottica primaria in *Plesrodotes walshii*. *Boll. dell'Ist. di Zool.*, R. Univ. Roma, vol. 5, pp. 1-83.
- . 1927b. Sul trapianto dell'occhio nei vertebrati. *Riv. di Biol.*, T. 9, pp. 515-523.
- . 1929a. Fenomeni di regolazione e di riparazione nello sviluppo dell'occhio degli anfibi. *Rend. R. Accad. dei Lincei, Cl. Sci. fis., mat. e nat.*, vol. 9, Ser. 6a, pp. 99-104.
- . 1929b. A proposito di trapianti embrionali. *Monit. Zool. Ital.*, T. 40, pp. 263-269.
- PETERSEN, H. 1923-1924. Berichte über Entwicklungsgemechanik. I. Entwicklungsgemechanik des Auges. *Ergeb. d. Anat.*, Bd. 24, S. 327-347; Bd. 25, S. 623-660.
- PHILLIPS, 1889. Monstres cyclopes chez les mammifères. *Jour. de l'Anat. et de la Phys.*, T. 25, pp. 67-105.
- V. QUEMNER, F.R. 1925. Über cyclocephale Larven von *Salamandra maculosa*. *Arch. f. Entsch.*, Bd. 105, S. 610-632.
- RABAUD, E. 1901-2. Recherches embryologiques sur les Cyclocephaliens. *Jour. de l'Anat. et de la Phys.*, T. 37, pp. 345-364, 575-594; T. 38, pp. 35-84, 282-315.
- RAVEN, C. P. 1933. Zur Entwicklung der Ganglienleiste. III. Die Induktionsfähigkeit des Kopfganglienleistenmaterials von *Rana fusca*. *Arch. f. Entsch.*, Bd. 130, S. 517-561.
- REIBER, G. 1508. *Margarita Philosophica*. Basileae. J. Schottus.
- ROUX, W. 1888. Ueber die künstliche Hervorbringung "halber" Embryonen. . . . *Virchow's Arch.*, Bd. 114, S. 113-291.
- SCHWALBE, E., und H. JOSEPHY. 1913. Die Zyklopie. In—Schwalbe, E.: Die Morphologie der Massbildungen, III. Teil, I. Abt., S. 205-246.
- SEKELDER, R. 1908. Zur Kenntnis der pathologischen Anatomie und Pathogenese der Zyklopie. *Arch. f. Ophth.*, Bd. 65, S. 242-274.
- . 1927. Die angeborenen Anomalien und Missbildungen des Auges. Kritischer Literaturbericht, umfassend den Zeitraum von 1913-1925. *Ergeb. Allgem. Path. u. path. Anat.*, Bd. 21, S. 511-629.
- . 1930. Die Missbildungen des menschlichen Auges. In: Schieck, F., und A. Brückner: Kurzes Handbuch der Ophthalmologie, Bd. 1. *Berlin*.
- SPEER, —. 1819. De Cyclopia sive Unione Partium Capitis in Statu Normali Disjunctarum. Diss. *Halen*. (Cited from Meckel, 1826.)
- SPEMANN, H. 1901a. Über Korrelationen in der Entwicklung des Auges. *Verh. ant. Ges.*, 15, Vers., Bonn, S. 61-79.
- . 1901b. Entwicklungsphysiologische Studien am *Triton-Bi*. I. *Arch. f. Entsch.*, Bd. 12, S. 224-264.
- . 1902. Entwicklungsphysiologische Studien am *Triton-Bi*. II. *Arch. f. Entsch.*, Bd. 15, S. 448-534.
- . 1903a. Entwicklungsphysiologische Studien am *Triton-Bi*. III. *Arch. f. Entsch.*, Bd. 16, S. 551-631.
- . 1903b. Über Linsenbildung bei defekter Augenblase. *Anat. Anz.*, Bd. 23, S. 457-464.
- . 1904. Über experimentellerzeugte Doppelbildungen mit cyclopischem Defekt. *Zool. Jahrb.*, Suppl. Bd. 7, S. 429-470.
- . 1912a. Zur Entwicklung des Wirbeltierauges. *Zool. Jahrb.*, Bd. 32, S. 1-98.
- . 1912b. Über die Entwicklung umgedrehter Hirnteile bei Amphibienembryonen. *Zool. Jahrb.*, Suppl. Bd. 15, III, S. 1-48.
- . 1918. Über die Determination der ersten Organanlagen der Amphibienembryonen. I-VI. *Arch. f. Entsch.*, Bd. 43, S. 448-555.
- . 1921. Die Erzeugung tierischer Chimären durch heteroplastische embryonale Transplantation zwischen *Triton cristatus* und *taeniatus*. *Arch. f. Entsch.*, Bd. 48, S. 533-570.

- SPEMANN, H., und H. MANGOLD. 1924. Über Induktion von Embryonalanlagen durch Implantation artfremder Organisatoren. *Arch. f. mikr. Anat. u. Entw. mech.*, Bd. 100, S. 599-638.
- SPEMANN, H., und E. BAUTZMANN. 1927. Über Regulation von *Triton*-Keimen mit überschüssigem und fehlendem medianem Material. *Arch. f. Entw. mech.*, Bd. 110, S. 557-577.
- SPEMANN, H. 1931. Über den Anteil von Implantat und Wirtskern an der Orientierung und Beschaffenheit der induzierten Embryonalanlage. *Arch. f. Entw. mech.*, Bd. 123, S. 389-517.
- STOCKARD, C. R. 1907a. The artificial production of a single, median cyclopean eye in the fish embryo by means of sea water solutions of magnesium chloride. *Arch. f. Entw. mech.*, Bd. 13, S. 249-258.
- . 1907b. The influence of external factors, chemical and physical, on the development of *Fundulus heteroclitus*. *Jour. Exp. Zool.*, vol. 4, pp. 165-201.
- . 1908. The question of cyclopia. *Science*, N.S. vol. 28, pp. 455-456.
- . 1909a. The artificial production of one-eyed monsters and other defects, which occur in nature, by the use of chemicals. *Anat. Rec.*, vol. 3, pp. 167-173.
- . 1909b. The development of artificially produced cyclopean fish.—"The magnesium embryo." *Jour. Exp. Zool.*, vol. 6, pp. 285-337.
- . 1910a. The influence of alcohol and other anaesthetics on embryonic development. *Am. Jour. Anat.*, vol. 10, pp. 369-392.
- . 1910b. The experimental production of various eye abnormalities and an analysis of the development of the primary parts of the eye. *Arch. vergl. Ophth.*, Bd. 1, S. 473-480.
- . 1913a. Location of the optic anlage in *Amblystoma* and the interpretation of certain eye defects. *Proc. Soc. Exp. Biol. and Med.*, vol. 10, pp. 162-164.
- . 1913b. An experimental study of the position of the optic anlage in *Amblystoma punctatum*. *Am. Jour. Anat.*, vol. 15, pp. 253-289.
- . 1914. The artificial production of eye abnormalities in the chick embryo. *Anat. Rec.*, vol. 8, pp. 33-41.
- . 1921. Developmental rate and structural expression: an experimental study of twins, double monsters, and single deformities, and the interaction among embryonic organs during their origin and development. *Am. Jour. Anat.*, vol. 28, pp. 115-266.
- STRANDBERG, G. L. 1922. The development of the auricle in the human embryo. *Carnegie Inst. of Washington, Contributions to Embryology*, vol. 14, pp. 111-138.
- Carnegie Inst. of Washington, *Contributions to Embryology*, vol. 22, pp. 1-44.
- STÄDER, W. F. H. 1933. Experimentelle Untersuchungen über die Mundentwicklung bei den Urodelen. *Arch. f. Entw. mech.*, Bd. 130, S. 131-186.
- TRUNGER, F. 1927. Contributo alla conoscenza della regolazione e fusione delle vescicole oculari in *Triton cristatus*. *Boll. Ist. Zool. Univ. Roma*, vol. 5, pp. 115-124.
- TRUDA, SE. 1924. Über eine zyklische Fehlbildung bei *Salamandra maculosa*. *Fol. Anat. Jap.*, vol. 2, pp. 107-118.
- VOGT, W. 1925. Gestaltungsanalyse am Amphibienkeim mit örtlicher Vitalfärbung. I. Teil. Methodik und Wirkungsweise der örtlichen Vitalfärbung mit Agar als Farbstoffträger. *Arch. f. Entw. mech.*, Bd. 106, S. 542-610.
- . 1929. Gestaltungsanalyse am Amphibienkeim mit örtlicher Vitalfärbung. II. Teil. Gastrulation und Mesodermbildung bei Urodelen und Anuren. *Arch. f. Entw. mech.*, Bd. 120, S. 384-706.
- VOLCK, W. 1849. Tabulae ad Illustrandam Embryogenesin Hominis et Mammalium tam Naturalem quam Abnormem. *Amstelodami*, G. M. P. Londonck.
- WACHE, H. 1920. Über Augenoperationen an Amphibienlarven. *Sitzungsber. d. Ges. naturf. Freunde zu Berlin*, S. 133-154.
- WEBER, E. I. 1915. Experimental studies aiming at the control of defective and monstrous development. A survey of recorded monstrosities with special attention to the ophthalmic defects. *Anat. Rec.*, vol. 9, pp. 529-562.
- . 1916a. Blastolysis as a morphogenetic factor in the development of monsters. *Anat. Rec.*, vol. 10, pp. 258-262.
- . 1916b. Experimental studies on the origin of monsters. I. An etiology and an analysis of the morphogenesis of monsters. *Jour. Exp. Zool.*, vol. 21, pp. 485-573.
- WILDER, H. H. 1908. The morphology of *Cosmobia*. *Amer. Jour. Anat.*, vol. 8, pp. 355-440.
- WOERDEMAN, M. W. 1929. Experimentelle Untersuchungen über Lage und Bau der augenbildenden Bezirke in der Medullarplatte beim Axolotl. *Arch. f. Entw. mech.*, Bd. 116, S. 220-241.
- . 1933. Über den Glykogenstoffwechsel des Organisationszentrums in der Amphibiengastrula. *Proc. Konink. Akad. Wetensch., Amsterdam*, vol. 36, pp. 189-193.
- WRIGHT, S., and O. N. RATON. 1923. Factors which determine otocephaly in guinea pigs. *Jour. Agr. Res.*, vol. 26, pp. 161-182.
- WRIGHT, S., and K. WAGNER. 1934. Types of subnormal development of the head from inbred strains of guinea pigs and their bearing on the



## ABERRANT FEEDING BEHAVIOR AMONG INSECTS AND ITS BEARING ON THE DEVELOPMENT OF SPECIALIZED FOOD HABITS

By CHARLES T. BRUES

*Harvard University*

THE behavior of insects with relation to food is extremely diverse if we consider them as a group. Any survey of its component parts reveals at once a more or less orderly distribution of the several types of food-habits with reference to characteristic peculiarities of structure, development and instinct. The dependence of trophic behavior upon the adjustment of such intrinsic factors to the environment is obvious, and we must look for any indications of the origin and development of predatism, vegetarianism, parasitism and the like by inquiry into the interactions of these internal and external modifications.

Diversity in behavior among insects is readily traceable to their extremely plastic structural organization which admits of many drastic changes in the form of bodily parts, such as the mouthparts, legs, respiratory system, wings, etc. Such structural peculiarities frequently appear without associated modifications in other structures and correspond almost invariably to changes in habits to which they are highly, often exquisitely adapted. Whatever theoretical interpretation we may apply to the origin of these adaptations, their occurrence is real and by no means infrequent. Many cases of peculiar food-relations appear to be primarily of this nature.

The indirect development of the higher insects opens new avenues for the initiation of profound although transitory

structural modifications in the nymphal and larval stages, since the latter are interpolated in such a way that they may develop at this time entirely novel characteristics which leave no impress upon the imago.

The writer has previously dealt at some length with many of these phenomena and the reader is referred to this earlier paper (*The Classification of Insects with Reference to the Characters of the Larva and Pupa*) published in the *Biological Bulletin*, vol. 37, pp. 1-21 (1919).

Similarly, hypermetamorphosis, which is particularly associated with developmental changes in food-habits, results in a differentiation of even the several larval stadia into divergent types, and quite independently of one another. Thus the food relations of a single individual may pass through several distinct, often radically different phases, each adapted to the requirements of life at a particular time.

The part played by modifications of instinct is the most difficult to comprehend, yet these continually intrude as a subtle background in any picture we may form of the food-habits of an insect. Here indeed, instinct appears frequently to transcend any materialistic considerations, at least of the kind which we as humans apply either to the epicurean selection of food, or to its choice on a nutritional basis.

As I believe that the account included on the following pages throws some light on the rôle of instinct in this connection,

it seems best to defer any more detailed statement until this material has been presented.

The food-habits of most insects as well as other animals fit quite readily into some one of the types that are inscribed at the four corners of the accompanying chart (Fig. 1). There always remains a residuum of forms which do not fall

mentally from the typical representatives of the remaining group. Finally the four types are not entirely coördinate in extent or range. By and large, however, they serve very well for most purposes of comparison and each includes a wide series of insects.

On our chart the sequence of these four types is: Saprophagy, Phytophagy, Preda-

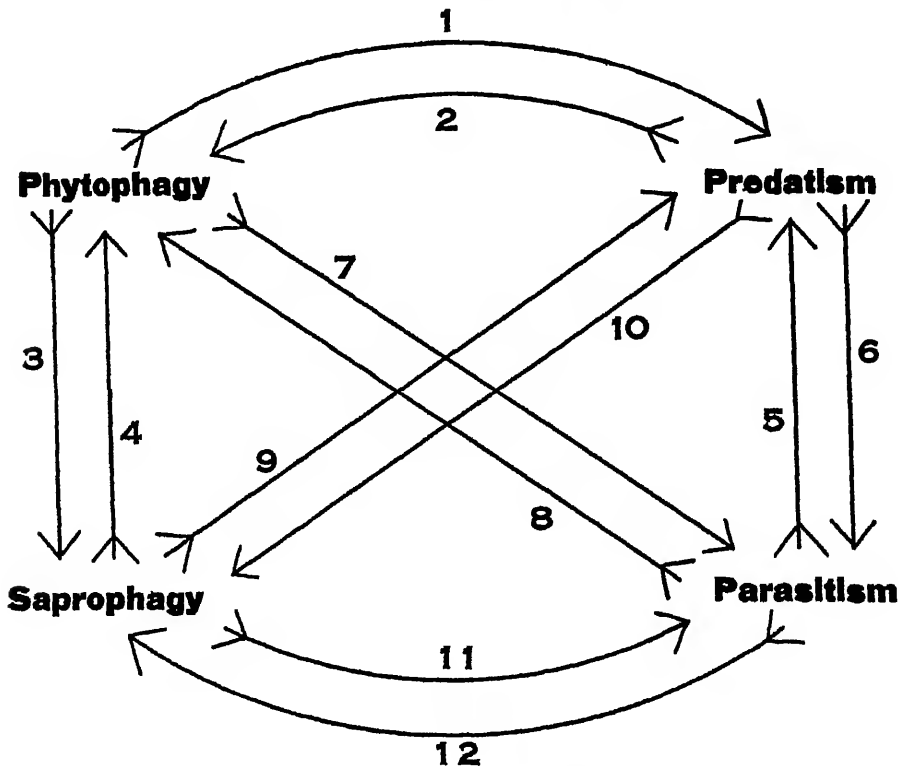


FIG. 1. DIAGRAM OF CHANGES IN FOOD HABITS

decisively into any one group; some of these combine more than one type, as phytophagy and saprophagy; some may be regarded as predators or parasites, dependent upon our exact definition of these two terms; others may pass from one to another during ontogeny; and again some are so highly specialized that although easily excluded from three categories they still differ quite funda-

tism and Parasitism. It would be difficult to present any conclusive evidence to prove that any one of the first three is more primitive than the others although I believe that the order given is probably correct at least for the terrestrial winged insects. In the case of the amphibiotic orders with aquatic nymphs like the may-flies and stone-flies it is quite possible the earliest forms were entirely sapro-

phagous. Since primitive types of both these series like the mantids and dragonflies are predatory this method of feeding undoubtedly arose very early in the history of insects. However, since the food of such insects consists mainly of other insects, predatism in its present form must represent a derived method of feeding.

Among living insects several orders are preëminently phytophagous and several are entirely or generally predatory. Parasitic and saprophagous forms are more commonly restricted to smaller groups, usually superfamilies or families, and one type or another frequently appears in a small part of a group where it is otherwise unknown. Thus among Lepidoptera, the caterpillars are constantly vegetarian, except for a few genera that have become carnivorous or predatory. Again in the several superfamilies that form the parasitic Hymenoptera a few scattered forms have adopted a purely vegetarian diet. The more closely we examine the food habits of insects, the more evident does it become that many shifts of this nature have occurred. These often represent quite complete reversals of habit and they are not generally connected by intergrades with the habits of the groups from which they have undoubtedly arisen. Once such a change has occurred, the new habits show the same remarkable constancy that characterizes the food-habits of insects in general.

I have indicated by arrows on the chart the shifts which may occur when any species changes from one method of feeding to another and it will be seen that twelve ways are possible between the four designated types. It is a simple matter to recall numerous instances of most of these possible shifts, although some occur much more frequently than others.

With these generalized statements before

us, we may enquire more closely into some specific cases which illustrate such shifts or sudden changes in food-habits. To avoid any doubt or ambiguity as to facts, care has been taken to disregard any observations that are not fully authenticated, however probable their accuracy may be, and furthermore, for the sake of brevity only four of the aforementioned twelve types of shifts are dealt with.

#### I. CHANGE FROM PHYTOPHAGOUS TO PREDATORY HABITS

The Lepidoptera probably furnish the best example of predatory habits arising in a few scattered members of an enormous group of insects where the larval stages are almost uniformly vegetarian. These sudden shifts in food-habits are still more remarkable when we recall that the diet of the phytophagous types is commonly greatly specialized by restriction to particular food-plants.

The following very brief account includes a summary of the habits of some of the Lepidoptera which have renounced the vegetarian habit to become carnivorous. In numerous instances there remain details yet to be elucidated, and undoubtedly many additional cases will be discovered as the life-histories of the Microlepidoptera become better known.

The larvæ of a number of butterflies are known to be predatory or at least highly carnivorous. These are very generally distributed throughout the world, but all belong to a single family, the Lycænidæ. Two subfamilies (Gerydinæ and Lipyrinæ) probably contain only carnivorous species, while a few members of another (Lycæninæ) lose the vegetarian habit characteristic of the remainder of the family only during the last larval instar. Thus a comparatively small group of butterflies exhibits very clearly a complete shift from plant to animal food. The habits of these



aberrant forms are summarized by Clark ('26) in a very complete paper from which many of the following notes have been drawn. Although a knowledge of carnivorous habits in any butterfly larva dates back scarcely half a century, the observations of many entomologists (1) have been required to accumulate the still meagre information now available. (The numbers in parentheses refer to the sections of the classified list of literature at the end of the paper.) The food-habits of ten genera and about fifteen species are at least fairly well known and these show very considerable diversity. In all cases there is a rather clear association with either Homoptera (Coccids, Aphids, Tree-hoppers or Leaf-hoppers) or with Ants, or more usually with both Homoptera and ants. The latter type of biocœnosis really represents the addition of the lycænid caterpillar to the more familiar and widespread association of ants with Homoptera. From the known facts it is not easy to determine, however, just how the peculiar relations now existent have arisen. Since many caterpillars of the strictly phytophagous Lycænidæ have frequently been observed to show strong cannibalistic tendencies we may infer that this led to the adoption of carnivorous habits in forms that feed upon aphids or coccids. One of these is the North American *Femisea tarquinius* whose larvæ live in colonies of *Schizoneura tessellata* on alder and in those of similar woolly aphids on other plants. Similar relations exist in the genus *Spalgis*, of which an Indian species, *E. epius* and also an African one, *E. lemolea* feed on mealy-bugs (*Pseudococcus*). As these aphids and mealy-bugs are regularly attended by ants it is but another step to a more intimate association with those ants which regularly build shelters over Homoptera. This is illustrated by several African species, *Megalo-*

*palpus zymma*, *Aslanga vininga*, and *A. lamborni* which feed on leaf-hoppers, tree-hoppers and lecanioid coccids. In an Australian form, *Liphyra brassolis*, the caterpillars have become myrmecophagous, living in nests of the fierce tree ant, *Ecophylla* on whose larvæ they feed, apparently accepted rather unwillingly by the ants but partially protected by their slug-like form and scuted integument. Finally a symphilic type of myrmecophily appears in an African form, *Euliphyra mirifica* in which the caterpillar has developed a snout-like head, which is thrust into the ant's mouth demanding food. This is forthcoming, although only in small quantities, necessitating a rather prolonged period of larval growth.

Among the carnivorous Lycænidæ there still remain certain forms, such as two British species of *Lycana* (*L. arion* and *L. alcon*) which are vegetarian as young caterpillars, but enter the nests of ants during the last larval instar where they become carnivorous and feed on the larvæ of the ants. In their later stages these caterpillars are provided with honey glands and are attended by ants even before they enter their nests. This type does not appear to be derived from the series mentioned previously and must represent an independent development of carnivorous habits.

In all the carnivorous lycænid caterpillars noticeable structural adaptations occur. Those in members of the first group involve great modification in body form or a thickening of the cuticle, and in the second group they are restricted mainly to the development of special glands like those occurring in various other myrmecophiles. It is noteworthy also that the adult butterflies of some of the carnivorous lycænidæ feed upon honey dew secreted by the same species of aphids that are eaten by their larvæ.

Similarly, among several other families of Lepidoptera the predatory habit appears in the caterpillars of a number of moths, mainly of the tineoid series. The erratic distribution of these cases with reference to taxonomic affinities indicates at once that we have to deal with the independent origin of this habit in several unrelated groups. The caterpillars of one entire family, the Epipyropidae (2) are, so far as is known, all carnivorous, feeding on various Homoptera (Jassoids, Fulgoroids and Scale Insects) and usually remaining attached to the body of the host during their entire period of growth. The head and mouthparts are much modified for sucking the juices of their prey and as the family enjoys a wide distribution in India, Japan, Australia and both Americas, predatism here is undoubtedly of long standing. This view is further substantiated by the incipient hypermetamorphosis, as the larva is more or less campodeiform when hatched, but later degenerates into an inactive, hemispherical grub.

In North America the caterpillars of several small moths feed on coccids (3). *Euclemensia bassettella*, an aberrant member, of the tineoid family Heliodinidae is a common enemy of the large oak-infesting, gall-like coccids of the genus *Kermes*, feeding within the body of its host (Comstock, '81; Hollinger and Parks, '19). *Holcocera iceryaella* of the family Blastobasidae, which similarly attacks various coccids in California, is thought probably to feed to some extent (Essig, '16; Basinger, '24), on dead specimens, wax-scales, etc. In India a species of *Holcocera* (*H. pulverea*) feeds on lac, affecting both living lac insects and stored lac (Ramakrishna Ayyar, '29). In India and Australia, Heliodinidae (Fletcher, '20; Tillyard, '26) of the genus *Strathmopoda* are coccidivorous, although the genus contains also vegetarian species in both these

regions, and in India the related *Edematopoda* includes both predatory and phytophagous forms. In one Australian species of *Strathmopoda* the food consists of the eggs of spiders, recalling the North American *Dicymolomia julianalis* (Gahan, '09; McCreary, '30) belonging to still another family (Pyralidae) whose larvae feed on eggs of the bagworm (*Thyridopteryx*), each caterpillar invading the larval case of the bagworm that contains the egg mass of the host. In the same family, Pyralidae, an Indian member of the Phycitinae (*Phycita dentilinella*) is carnivorous, feeding on pupae of a Eucleid moth as well as those of a wild silkworm, *Cricula trifenestrata* (Ramakrishna Ayyar, '29).

The Noctuidae also contain at least two well known genera with carnivorous habits. These are *Eublemma* which contains numerous Indian species that feed on scale insects of various kinds, and the Australian *Catablemma* (Froggatt, '10; Tillyard, '26) with similar habits. In connection with the predatory habit in this family it is interesting to note that its members seem to be especially prone to exhibit cannibalistic tendencies (Berg, '92; Brues, '20; Lommatsch, '26; Moore, '12), although this phenomenon is by no means restricted to them.

Perhaps most remarkable among the predatory lepidopterous larvae is *Cyclotorna*, sole representative of the peculiar Australian family Cyclotornidae. Five species are known from Queensland (Dodd, '12), several of which, and probably all, are predatory on leaf-hoppers during early larval development and later feed on the larvae of ants. In the case of *Cyclotorna monocentra* as discovered by Dodd, the eggs are deposited on the twigs of trees and the young larvae feed by attaching themselves to the bodies of nymphal jassids which are present on the trees. The larvae remain

active and may shift from one host to another; after a period of growth they spin a silken cocoon from which the caterpillar emerges after having undergone some changes. This caterpillar then induces a worker of the common ant, *Iridomyrmex purpureus* which frequents the trees where the jassids occur, to carry it to the ant's nest. Here it completes its feeding at the expense of the ant-larvæ. It thus appears probable that the caterpillar is predatory during its entire development, as its behavior on the jassids does not suggest that it feeds upon the sweet secretions which serve to attract the ants.

A survey of predatory habits might be extended into other groups that are primarily vegetarian as many such have often been observed, but they are quite similar to those just mentioned. It is, however, of interest to find that the Orthoptera (*sensu stricto*), which are much less highly specialized with reference to food than the Lepidoptera, show comparable digressions. This has been repeatedly noted in various parts of the world among the long-horned grasshoppers of the family Tettigoniidæ (Locustidæ), particularly members of the Conocephalinæ (Xiphidiinæ) (4). In North America species of *Orchelimum* have been observed to eat beetles, moths and other Orthoptera and in Hawaii *Gonocephalus* commonly feeds on leafhoppers, mealy-bugs and pupæ of moths. In Natal, caterpillars of a stalk-borer (*Busseola fusca*) are frequently eaten by a related grasshopper (*Clonia vittata*). Even certain wingless Stenopelmatidæ, as *Udopsylla nigra*, readily consume may-beetles, other Coleoptera and grasshoppers.

Among the Orthoptera these aberrant habits are less firmly fixed than they are in most Lepidoptera as a vegetarian diet is only supplemented by animal food at

times, occasionally to such an extent that plant food may be practically eliminated. As cannibalistic tendencies are here often evident and as the prey frequently consists of related Orthoptera, it is not surprising to find this taste for animal food, particularly as the mouthparts are unusually well adapted for the purpose in the Conocephalinæ, to which most of the records relate.

Turning to a more specialized order like the Hymenoptera where the lower forms are phytophagous, carnivorous aberrations frequently occur among adult sawflies. This is attested by numerous observations (5) of these insects, which are known to capture and eat other kinds of insects.

## II. CHANGE FROM PREDATORY TO PHYTOPHAGOUS HABITS

The appearance of phytophagous habits in a family of typically predatory insects is well exemplified by the Coccinellidæ (6), an extensive group of small beetles. With the exception of one very discrete series, these insects subsist almost entirely on other insects that are devoured by larvæ and adults alike. Disregarding for the moment two minor groups and a few scattered cases, the phytophagous forms, which represent without doubt the derived type, form a subfamily, Epilachninæ. Our present knowledge of their food-habits is confined to certain representatives of the large, cosmopolitan genus *Epilachna* and of two related genera, *Subcoccinella* and *Cynogastis*. They are purely vegetarian and show the same specificity in choice of food-plants that is characteristic of other phytophagous beetles, such as the Chrysomelidæ. The habits of about fifteen species are well known through the observations of numerous entomologists (Del Canizo, '28; Chue, '30; Den Droop, '18; Fletcher, '14; De Fonseca and Autuori,

'31; Friend and Turner, '31; Froggatt, '21; Howard and English, '24; Klemm, '29; Korschewsky, '29; Krishnamurti, '32; Murum tsu, '19; Schilder, '28, '29; Stroubal, '26; Subramaniam, '24; Takagi, '32; Tanabe and Sekiya, '31; Veitch, '31) as some are economically important pests in both the New and Old World.

In North America we have two abundant species of *Epilachna* one of which, *E. borealis*, feeds mainly on the foliage of our native wild cucumber, *Echinocystis lobata*, but also commonly affects certain introduced cucurbits in gardens such as squash and pumpkin. The other, *E. corrupta*, which has recently extended eastward into the Atlantic States from the Southwest, is known as the Mexican bean-beetle since it feeds generally on various beans and more sparingly on some other leguminous herbs. In Europe two common forms, *E. chrysomelina* and *E. undecimmaculata* occur on cucurbits, the latter generally restricted to native species of *Bryonia* and *Echallium*. No European species of *Epilachna* is known to attack beans or other Leguminosæ, but the related *Subcoccinella vigintiquatuorpunktata* feeds regularly on alfalfa, and sparingly on certain other unrelated plants of several families, e.g., *Saponaria*. In Europe another food-plant appears in the dietary of *Epilachna*, for *E. chrysomelina* sometimes appears abundantly on potato foliage when the preferred cucurbitaceous plants are absent. Passing now to Eastern Asia, India, Japan, Malaya and Australia we find two general types of food preference exhibited by several species of *Epilachna* that occur in these regions. *E. vigintioctopunctata*, which extends from India through southern China into Java, the Philippines and finally into Australia, feeds generally upon potatoes, often becoming a severe pest and appearing also on other solanaceous plants. These latter include tomato, several wild or intro-

duced species of *Solanum* as well as *Datura* and *Physalis*. In the western part of its range, however, it frequently appears on cucurbits, as we have noted is the case with the European and North American species, and once in Australia it has been found on cotton. Several other south Asiatic species likewise affect Solanaceæ. Similarly the Japanese *E. niponica* effects both Cucurbitaceæ and Solanaceæ, having been noticed particularly on the commonly grown garden vegetables belonging to this family, as well as rarely on unrelated plants such as cherry. In South America at least two species, *Epilachna clandestina* and *E. panulata* affect various cucurbits, but no forms feeding on Solanaceæ appear to have been reported from that continent. Finally, in Africa five species, *E. dahlbomi*, *E. godarti*, *E. matronula*, *E. polymorpha* and *E. similis* have been found feeding on cotton, a malvaceous plant not related to those previously mentioned (except single recorded instances of *Epilachna* on cotton in Australia and Malaya) showing the existence of another type of food preference among the Ethiopian species of *Epilachna*. I have outlined in some detail the food preferences of *Epilachna* as they show transitions that indicate a remarkably clear correlation between distribution and food-plants.

In one other tribe of Coccinellidæ, the Veraniinæ, five species feed on Gramineæ and represent a second independent shift from predatory habits.

A further independent development of phytophagy of a specialized type is seen in another small series of Coccinellidæ where several genera have become mycophagous. This habit has been frequently observed in species of *Tbaa*, *Vibidia* and *Halysia*, (Lichtenstein, '17; Martelli, '10-'14; Stroubal, '26; Tokura and Kakuta, '30), all of which belong to the tribe Psylloborini. Here the food consists gen-

erally of the spores as well as conidia and perithecia of various fungi (Tetrasporiales and Mucedineæ).

Some other observations indicate that vegetable material such as pollen occasionally enters into the dietary of other coccinellids or that they may very exceptionally feed to some extent on foliage (Brassler, '30), but such behavior appears to have no definite status so far as the general habits of species are concerned.

### III. CHANGE FROM PHYTOPHAGOUS TO SAPROPHAGOUS HABITS

Certain Lepidoptera serve very well to illustrate modifications in food habits where plant food is replaced by dead organic matter of animal origin. This method of larval sustenance is of course painfully evident in the case of our common clothes moths and it extends to certain related forms as well as to other more widely different members of the order. Clothing is not a direct product of nature, but the materials from which it is made are but little changed during the process of manufacture, particularly in the case of woollen, fur and feather garments, so that it is to these that we must go to search for the origins of such household pests and their associates under natural conditions. The food of the caterpillars of the two common clothes moths (*Tineola biselliella* and *Tinea pellionella*) is generally confined to animal fibers: fur, wool and feathers derived from the higher vertebrates and containing keratin. Silk and vegetable fibers are quite consistently refused, although various materials may serve for at least partial development and the caterpillars have even been reported on occasion to become predatory and feed on mites (Webster, '17), or even become cannibalistic, feeding on pupæ of their own species (Illingworth, '17). A reported infestation of sugar (Dingler,

'28) may perhaps involve this carnivorous habit also. The natural occurrence of related forms as epizotic parasites where they feed in the fur of mammals, is well known. A group of pyralidid moths feed as larvæ on the fur of living sloths. These belong to three related neotropical genera, *Cryptoses*, *Bradypodicola* and *Bradypophila*, extending from Central America into Brazil where they have been found on numerous occasions (Dyar, '08a, '08b, '12; Goeldi, '93; von Ihering, '14; Spuler, '06), always in this very unusual habitat. Another moth with comparable habits is *Tinea vastella*, a case-forming moth described by Busck ('10) from East Africa. In this case the larvæ burrow into the horns of antelopes where they feed on materials closely similar to those utilized by the fur-moths.

The normal food nutriment of the caterpillars of both species of clothes moths is the keratin present in the animal hairs (Sitowski, '05; Schulz, '25). It is, however, evident that many other materials (Colman, '32; Fricklinger, '20; Griswold, '33) suffice in view of the occasional predatory behavior observed, as well as the occurrence of larvæ in boxes of dried insects. Moreover, their rapid development in fish-meal and an acceleration of growth noticed on the addition of dried yeast to their food indicates quite positively that they are not limited to any specific type of food. This is further demonstrated by *Tineola uterella*, known to feed on dried fruits as well as woollen material (Kca, '33). The same is true of numerous other tineids, particularly many case-bearing forms which are scavengers. Sometimes more definite associations are formed as in the case of an oecophorid, *Neossiosynaca scatophaga* (Turner, '23) which has been found in parrots' nests in Queensland.

Another development of saprophagy

among Lepidoptera occurs in the subfamily Galleriinae of the Pyralidae, two members of which (*Galleria mellonella* and *Achroia grisella*) live as caterpillars in hives of the honey-bee (8). These are appropriately known as wax moths since the larvae subsist upon the waxen comb in combination with refuse material such as larval and pupal exuviae, excreted nitrogenous material and the like (Borchert, '33; Dickmann, '33; Kranche, '33; Kunicke, '30; Manunta, '33; Metalnikov, '08; Röber, '33; Sieber and Metalnikov, '04). Wax is an essential part of their diet. These species are thus true scavengers and their habits are firmly fixed as inquilines in the hive. Curiously enough *Achroia grisella* has been reared successfully (Görze, '29) from the seeds of a wide variety of herbs and trees, but this is by no means a normal habit.

#### IV. CHANGE FROM PARASITIC TO PHYTOPHAGOUS HABITS

Perhaps the case that will illustrate best the development of phytophagy in a group of ordinarily parasitic insects is a series of chalcid-flies that are plant-feeders (9). The vast majority of the forms which constitute this superfamily of Hymenoptera are entomophagous parasites affecting the eggs, larvae or pupae of very diverse insects in many different ways. As the group is extremely large and complex it presents great difficulties to the taxonomist, while the generally small or minute size of the individual insects makes the study of their life histories slow and arduous. Since the parasitic chalcid-flies are very important in regulating the abundance of many economically important insects and the phytophagous forms include a number of destructive pests, the habits of a large number of species have been carefully worked out until we now have a fairly accurate notion of the way in

which parasitism and phytophagy appear within the group.

On account of the great preponderance of parasitic types among the existing species of Chalcidoidea, the obvious supposition is to regard the phytophagous habit as secondary or derived. An interest and slight acquaintance of the group, extending over many years, has convinced me that this has indeed been the course of evolution and that certain originally parasitic types have adopted a fixed vegetarian diet. This conclusion has been reached and very adequately defended by Gahan ('22) on the basis of a wide personal knowledge of both the taxonomy and the biology of the group. The main evidence for the validity of this view depends upon the following facts: 1) Phytophagy appears in an erratic way in at least six (excluding the entirely vegetarian fig-insects) of the fifteen or more families into which the Chalcidoidea are usually divided. 2) The phytophagous forms are always similar to the prevailing parasitic types in each family, less numerous in species and sometimes so closely related that they may not show even generic differences; in other words, the phytophagous forms show little morphological change corresponding to their habits, indicating their recent development. 3) Some species are parasitic during early life, later feeding to maturity on plants. This has been shown to be the case among certain Eurytomidae (Rimsky-Korsakow, '14; Phillips, '17; Nielsen, '06) of the genera *Eurytoma* and *Harmolita*, both of which include also numerous entirely vegetarian species that eat seeds or produce galls on grasses. This transition in food habits is particularly important in this connection and recalls the reverse condition we have already mentioned in lycænid caterpillars where phytophagy precedes predatism during

ontogeny. 4) The dependence of phytophagous chalcid-flies upon the seeds of plants is a natural transition since these are rich in fats and proteins, approaching in composition at least roughly the food of their parasitic relatives. The extensive genus *Megastigmus* and some of its allies of the family Callinomidae also develop in the seeds of plants, especially trees. The gall-makers appear to be, at least in some cases, related to forms that are parasites of gall insects, indicating some similarity in habitat and in the vegetable food to which their ancestors may have been accustomed, albeit in a metamorphosed condition, in the bodies of their gall-making hosts.

Why the chalcid-flies should have produced so many secondarily phytophagous forms while the other two large groups of parasitic Hymenoptera have not done so seems to find no explanation at the present time.

The larva of at least one species of Ichneumonidae (*Grotes anguina*) is mainly phytophagous. It was found many years ago by Graenicher ('05) in the nest of a bee (*Ceratina*) where it destroys the egg or first stage larva of the host-bee and later consumes the store of bee-bread in the nest, after the fashion of a parasitic bee; it then makes its way to an adjoining *Ceratina* cell to complete its growth at the expense of a second larva. The *Grotes* larva is of course entirely vegetarian after the killing of the minute bee-egg or first larva until it later attacks the larger second larva.

#### V. DISCUSSION

The foregoing account of aberrant food-habits among a variety of insects shows that many such cases have several features in common, in spite of dissimilarities which are everywhere apparent. Shifts in the basic methods of feeding have occurred frequently and have not appeared, so far as can be ascertained, on any predictable basis.

The difficulty of predicting the association of parasitic insects with their hosts on the basis of natural relationships has been pointed out by Thomp-

son and Parker (The Problem of Host Relations, with Special Reference to Entomophagous Parasites, *Parasitology*, vol. 19, pp. 1-34, 1927). These authors have not considered, however, the bearing of this on the origin of new host relations. Here the situation is not so clear since the mutual adjustments of host and parasite are much more complete than they are among the types of insects discussed in the present account.

It is true that some groups are more plastic than others in this respect and in a group where one unusual type has arisen, others are apt to be met with, as for example the generalized tincoids and specialized lycæ-nids among Lepidoptera. Two characteristics of these changed habits indicate conditions closely similar to those associated with mutations in the structure of bodily parts. The change very frequently appears to be sudden and complete and from the nature of the case such most often needs be true where a change of habitat is involved. Even without the latter complication it is certainly not the rule to find any species indiscriminate, for example in its use of animal and plant food. Such cases do occur, e.g., in the long-horned locusts mentioned earlier, but these do not appear to represent a step in the development of predatism, as a purely carnivorous diet has, so far as is known, not developed anywhere in the Orthoptera. A second characteristic feature of these shifts is their constancy when once established. They become hereditary and fixed for long periods. In the phytophagous coccinellids a sufficient time has elapsed for a whole subfamily with numerous genera and a great many species to become differentiated. Meanwhile no further shift in food-habits has occurred and the Epilachninae retain their acquired vegetarian appetites. One may only hazard a guess as to the time involved, but from our general knowledge of Tertiary insects it certainly runs into many millions of years.

Granted that these changes have since remained so firmly fixed in the genetic constitution of a group that they show no tendency to revert to the previous condition, we may ask whether they have a physiological basis. Are they dependent upon physiological necessity, in that they represent necessary or advantageous shifts from a nutritional or purely digestive standpoint? There is some experimental evidence on this phase of the question, but unfortunately it is not so far of adequate extent and there is no promise that it may soon be greatly extended. The application of any experimental method to determine the factors which underlie the choice or selection of foods as related to their actual availability is not easy when dealing with insects. We know only that certain, often very specific foods are acceptable, sometimes only a single species of plant and that offerings of anything else are steadfastly refused, even to the point that actual starvation supervenes. However certain we may be by analogy with other species that the experimental subjects are refusing foods perfectly appropriate for assimilation, their apathy recalls the jailed fanatic on a hunger strike and further experimentation is fruitless. The use of synthetic foods as media for some species and the addition of extracted substances from peculiar foods like beeswax in connection with the wax moth have demonstrated the actual necessity of some specific substances in certain cases, but the principal experimental data relate to more general matters such as vitamin requirements and furthermore they must usually be confined to species normally accustomed to variable or mixed diets. Although the possibility of physiological adaptation cannot be excluded as a primary factor, there seems to be no evidence that changed nutritional requirements precede shifts in food-habits or even that they are coincident with them.

Neither are shifts in food-habits necessarily preceded or accompanied by essential anatomical changes in the mouthparts or other organs which are more or less intimately connected with feeding. Frequently, of course, profound structural modifications appear in predators or parasites with very specialized habits, for example those previously mentioned in lycænid caterpillars where the symphylic honey-glands or snout-like head appear among these secondarily carnivorous larvae. As exactly similar modifications appear here and there in groups where no such shifts in habits occur, there is certainly no reason to believe that they precede rather than accompany or follow the specialized habits of their possessors. This is perhaps approaching dangerously near the oft-repeated query as to whether changes of form follow or precede changes in function, but it is clear that the present implication is quite different. Since in our present series morphological changes are not always present, they are not necessarily associated with shifts in habits, and we cannot therefore link the origin of changed habits with structural modification.

There remains the probability that many of the changes in food-habits which we have been considering are primarily due to changes in instinct which are neither dependent upon, nor correlated with changes of any other sort, either morphological or physiological. The instinctive selection of food by those insects which are definitely restricted to a limited dietary is in its perfected state infallible or practically so. The occasional instances observed where a species may lay its eggs on food which its larvae will not accept usually result in disaster for the offspring, although we have good reason to believe that quite generally the larvae might perfectly well grow to maturity were it not for their refusal to accept the unac-



customed food. Such aberrations are rare, but are more frequent than others where larvæ shift to strange food without any parental suggestion. We usually regard the instinctive selection of the food-plant by an ovipositing insect and the subsequent feeding of the larva on the food selected by the mother as phases of the same specific attachment to that particular plant. Certainly both actions are perfectly adapted to each other, and they must be coincident if the species is to continue in proper adjustment to its environment, but we have no assurance that they can never change independently.

Since it must be admitted that instinct is the determining factor both in selecting food plants and utilizing them, there seems to be only one conclusion that may be drawn. When the normal repetitive chain of these instincts is dislocated new food relations may appear. And further,

they may persist without discontinuous subsequent modification, as hereditary aberrations of these instincts are very rare. We must attribute the origin of the types of aberrant food habits dealt with on the preceding pages to basic hereditary changes in instinct. These have originated just as they have in purely phytophagous insects where some circumscribed series becomes dependent upon food-plants widely different from those utilized by the general group to which it belongs. Many cases of this sort are well known (Brues, '20).

It is difficult to appreciate the absolute rigidity of the instincts with which we are dealing and their consequent effects in preventing so completely the development of the more diversified food-habits found in most non-parasitic animals, including many insects.

#### LIST OF LITERATURE

This is in no sense a bibliography; it is intended only to indicate documentary sources which will furnish more extensive accounts of many of the observations referred to in this paper.

##### *Change from Phytophagous to Predatory Habits*

##### 1. Butterflies

- CHAPMAN, T. A. ('02) On the larva of *Liphyra brassolis* Westw. *Entomologist*, vol. 35, pp. 225-228; 252-255, 4 pls.
- CHAPMAN, T. A. ('14) The mystery of *Lycana arion*. *Entom. Rec. Journ. Var.*, vol. 26, pp. 245-246.
- CLARK, A. H. ('26) Carnivorous butterflies. *Ann. Rept. Smithsonian Inst., Washington*, 1925, pp. 439-508.
- DODD, F. P. ('02) Contribution to the life history of *Liphyra brassolis* Westw. *Entomologist*, vol. 35, pp. 153-156.
- FROHAWK, F. W. ('03) The earlier stages of *Lycana arion*. *Entomologist*, vol. 36, pp. 57-60.
- HOLLAND, W. J. ('92) The life-history of *Spalgis s-signatus* Holl. *Psyche*, vol. 6, pp. 201-203.
- KIRKALDY, J. C. W., and G. W. KIRKALDY. ('05) The anatomy and life-history of the homopterous insect *Pyrops candalaria*. *Zool. Jahrb. Abth. f. Syst.*, vol. 29, pp. 105-124.
- LAMBORN, W. A., et al. ('14) The relationship between certain West African insects. *Trans. Entom. Soc. London*, 1914, pp. 436-524, 4 pls.
- MANN, W. M. ('20) Ant guests from Fiji and the British Solomon Islands. *Ann. Entom. Soc. America*, vol. 13, pp. 60-69, 9 figs.
- RILEY, C. V. ('86) A carnivorous butterfly larva. *Science*, vol. 7, p. 394.

##### 2. *Epipyropidae*

- DYAR, H. G. ('02) A lepidopterous larva on a leaf-hopper, *Epipyrops barberiana* n.sp. *Proc. Entom. Soc. Washington*, vol. 5, pp. 43-45.
- DYAR, H. G. ('04) A Lepidopteron parasitic upon Fulgoridae in Japan. *Proc. Entom. Soc. Washington*, vol. 6, p. 19.
- PERKINS, R. C. L. ('05) Leaf-hoppers and their natural enemies (Pt. II. Epipyropidae). *Bull. Div. Entom., Hawaiian Sugar Planters' Expt. Sta.*, No. 1, pt. 2, pp. 85.
- BOWLING, J. C. ('05) [A curious coccus-like insect parasitic upon *Fulgura candalaria*.] *Proc. Entom. Soc. London*, (2), vol. 1, p. xxxvi.

## 3. Other Predatory moths

- BASINGER, A. J. ('24) A supposedly beneficial insect discovered to be a citrus pest. *Journ. Econ. Entom.*, vol. 17, pp. 637-639.
- BERG, C. ('92) Canibalismo entre insectos. *Anal. Soc. Cient. Argentina*, vol. 34, pp. 236-238.
- BRUES, C. T. ('20) The selection of food-plants by insects, with special reference to lepidopterous larvae. *American Naturalist*, vol. 54, pp. 313-332.
- COMBTOCK, J. H. ('81) Notes on predaceous Lepidoptera. *Rept. U. S. Comm. Agric.*, 1880, pp. 241-242.
- DODD, F. P. ('12) Some remarkable ant-friend Lepidoptera of Queensland. *Trans. London Entom. Soc.*, 1911, pp. 577-590.
- ESSIG, E. O. ('16) A coccid-feeding moth, *Holcocera iceryaella* (Riley) (*Blastobasis iceryaella* Riley). *Journ. Econ. Ent.*, vol. 9, pp. 369-370, 1 pl.
- FLETCHER, T. B. ('20) Life-histories of Indian insects. Microlepidoptera. *Mem. Dept. Agric. India, Entom. Ser.*, vol. 6, Nos. 1-9, 217 pp., 68 pls.
- FROGGATT, W. W. ('10) Scale-eating moths. *Agric. Gaz. New South Wales*, vol. 21, p. 801, 1 pl.
- GAHAN, A. B. ('09) A moth larva predatory upon the eggs of the bagworm. *Journ. Econ. Entom.*, vol. 2, pp. 236-237.
- HOLLINGER, A. H., and H. B. PARKS. ('19) *Euclemensia bassettella*, the *Kermes* parasite (Microlepidoptera, Tineoidea, Oecophoridae). *Entom. News*, vol. 30, pp. 92-100, 1 pl.
- MAHDIKASSAN, S. ('29) Schmetterlingsraupen als Feinde der Lackschildläuse. *Natur. u. Mus.*, vol. 59, pp. 394-400, 10 figs.
- MCCREARY, D. ('30) *Dicymolomia julianalis* Walk. predatory upon bagworm eggs. *Journ. Econ. Entom.*, vol. 23, p. 883.
- MOORE, H. W. B. ('12) Ways and habits of caterpillars. *Timbri* (3), vol. 2, pp. 197-206.
- PAONENRECHER, A. ('09) Die geographische Verbreitung der Schmetterlinge. ix + 451, pp., 2 maps. *Jms*, G. Fischer.
- RAMAKRISHNA AYYAR, T. V. ('29) Notes on some Indian Lepidoptera with abnormal habits. *Journ. Bombay Nat. Hist. Soc.*, vol. 33, pp. 668-675.
- TILLYARD, R. J. ('26) The Insects of Australia and New Zealand. *Sydney*, Angus and Robertson.

## 4. Predatory Orthoptera

- AKERMANN, C. ('32) On the carnivorous habits of the long-horned grasshopper, *Clonia vittata* Thunberg. *Ann. Natal Mus.*, vol. 7, pp. 143-144.
- BLATCHLEY, W. S. ('03) The Orthoptera of Indiana.

27th Ann. Rept. Dept. Geol. Nat. Res., Indiana, 471 pp.

- HANCOCK, J. L. ('04) The oviposition and carnivorous habits of the green meadow grasshopper. *Psyche*, vol. 11, pp. 69-71, 1 pl.
- ILLINGWORTH, J. F. ('29) Grasshoppers eat pineapple mealy bugs and other pests. *Proc. Hawaiian Entom. Soc.*, vol. 7, pp. 256-257.
- SMITH, R. C. ('20) Predaceous grasshoppers. *Journ. Econ. Entom.*, vol. 13, p. 491.
- SWEZEY, O. H. ('05) Leaf hoppers and their natural enemies, Pt. VII. *Bull. Hawaiian Sugar Planters' Exp. Sta.*, No. 1, pp. 211-238, 4 pls

## 5. Predatory Sawflies

- MRÁZEK, A. ('09) Fleischfressende Blattwespen. *Zeits. wiss. Insektenbiol.*, vol. 5, p. 245.
- ROHWER, S. A. ('13) Notes on the feeding habits of two adult sawflies. *Proc. Entom. Soc., Washington*, vol. 15, pp. 148-149.
- VENABLES, E. P. ('14) A note upon the food-habits of adult Tenthredinidae. *Canadian Entom.*, vol. 46, p. 121.

## Change from Predatory to Phytophagous Habit

## 6. Phytophagous Coccinellidae

- BRASLER, K. ('30) Ist *Coccinella 7-punctata* L. wirklich nur Blattlausfresser? *Zeits. Pflanzenkrankh.*, vol. 40, pp. 511, 513, 2 figs.
- DEL CAÑIZO, J. ('28) Una plaga de los melonares (*Epilachna chrysomelina* Fabr.). *Bol. Pes. Veg. Entom. Agric.*, vol. 3, pp. 124-130, 5 figs.
- CRUE, C. C. ('30) Some biological notes on a leaf-feeding coccinellid (*Epilachna 28-punctata*). *Liguan Sci. Journ.*, vol. 6, pp. 301-313, 11 figs.
- DERN DOOP, J. E. A. ('18) Levensgeschiedenis van *Epilachna dodocastigma* Mulsant, in Deli. *Teymannia, Batavia*, vol. 30, pp. 243-253, 1 pl.
- FLETCHER, T. B. ('14) Some South Indian insects, pp. 291-292. *Madras, Govt. Press*, 1914.
- DE FONSECA, J. P., and M. AUTUORI. ('31) Contribuição para a biologia de *Solenophila claudensina* (Muls.). *Revist. Entom.*, vol. 1, pp. 219-224, 5 figs.
- FRIEND, R. B., and N. TURNER. ('31) The Mexican bean beetle in Connecticut. *Bull. Connecticut Exp. Sta.*, no. 332, pp. 73-108, 14 figs., 15 tables.
- FROGGATT, W. W. ('21) Ladybird beetles and potatoes. *Agric. Gaz. New South Wales*, vol. 32, p. 196.
- HOWARD, N. F., and L. L. ENGLISH. ('24) Studies of the Mexican bean beetle in the Southeast. *Bull. U. S. Dept. Agric.*, no. 1243.

- KLEMM, M. ('29) Beitrag zur Morphologie und Biologie der *Epilachna chrysomelina* Fabr. *Zeits. wiss. Insektenbiol.*, vol. 24, pp. 231-251, 14 figs., 3 pls.
- KORSCHENSKY, R. ('29) Bemerkungen über afrikanische Epilachninen mit Beschreibung einer neuen Art. *Deuts. entom. Zeits.*, 1929, pp. 141-143, 2 figs.
- KRISHNAMURTI, B. ('32) The potato *Epilachna* beetle, *Epilachna vigintioctopunctata* Fabr. *Bull. Dept. Agric. Mysore, Entom. Ser.*, No. 9, 16 pp., 5 pls.
- LICHTEENTHIN, J. L. ('17) Observations sur les coccinellides mycophages. *Bull. Soc. Entom. France*, 1917, pp. 298-302.
- MARTELLI, G. ('10-'14) Sulla microfagia del coccinellide, *Thea xxii-punctata* L. *Boll. Lab. Zool. Portici*, vol. 4, pp. 291-294 (1910); [also] Notizie su due coccinellide microfagi. *Ann. R. Scuola. sup. Agric. Portici*, vol. 12, pp. 663-672 (1914).
- MURAMATSU, S. ('19) The life-history of *Epilachna niponica*. [In Japanese]. *Insect World, Gifu*, vol. 23, pp. 17-20.
- SCHILDER, F. ('28) Die Nahrung der Coccinelliden und ihre Beziehung zur Verwandtschaft der Arten. *Arbeit. biol. Reichsanst.*, vol. 16, pt. 2, pp. 213-282.
- SCHILDER, F. A. ('29) Die Beziehung der Nahrung der Coccinelliden zur systematischen Stellung der einzelnen Genera. *Congr. Internat. Zool.* 10, pt. 2, pp. 1018-1021.
- STROUBAL, H. ('26) Pilzfressende Coccinelliden (Tribus Psylloborini). *Zeits. wiss. Insektenbiol.*, vol. 21, pp. 131-143.
- SUBRAMANIAM, T. V. ('24) Some coccinellids of South India. *Proc. Fifth Entom. Meeting, Poona*, 1923, pp. 108-118.
- TAKAGI, S., and K. ITO. ('32) Studies on *Epilachna niponica* Lw. [In Japanese]. *Fukushima Agric. Exp. Sta.*, 50 pp., 1 pl.
- TANABE, C., and J. SEKIYA. ('31) On the biology of *Epilachna niponica*. [In Japanese]. *Repts. Nagano Agric. Expt. Sta.*, No. 2, pp. 1-15.
- TOKURA, S., and K. KAKUTA. ('30) Coccinellids feeding on fungi. [In Japanese]. *Nogaku Kenkyu*, vol. 14, pp. 243-245.
- VEITCH, R. ('31) The leaf-eating ladybird. *Queensland Agric. Journ.*, vol. 36, pp. 482-484, 4 figs.
- UNDERHILL, G. W. ('23) The squash lady bird (*Epilachna borealis*). *Bull. Virginia Agr. Exp. Sta.*, no. 232, 24 pp.
- by the larvae of two species of clothes moth, *Timola biselliella* and *Timus pallionella*. *Journ. Textile Inst.*, vol. 22, pp. T141-T157.
- BUCK, A. ('10) Notes on a horn-feeding lepidopterous larva from Africa. *Smithsonian Misc. Collect.*, vol. 56, No. 8, 2 pp., 2 pls.
- COLMAN, W. ('32) Effect of yeast on clothes moth larvae. *Journ. Econ. Entom.*, vol. 25, p. 1242.
- DINGLER, M. ('28) Merkwürdiges Auftreten einiger Hausschädlinge. *Anz. Schädlingssk.*, vol. 4, pp. 124-125.
- DYAR, H. G. ('08a) A pyralid inhabiting the fur of the living sloth. *Proc. Ent. Soc. Washington*, vol. 9, pp. 142-144.
- DYAR, H. G. ('08b) A further note on the sloth moth. *Proc. Ent. Soc. Washington*, vol. 10, pp. 81-82.
- DYAR, H. G. ('12) More about the sloth moth. *Proc. Ent. Soc. Washington*, vol. 14, pp. 169-170.
- FRICKLINGER, H. W. ('20) Die Kleidermotte (*Timola biselliella* Hummel) als Schädling in zoologischen Sammlungen. *Zeitschr. f. angew. Entom.*, vol. 6, pp. 400-404, 3 figs.
- GORDI, E. A. ('93) Os Mammíferos do Brasil. 180 pp. *Rio de Janeiro*.
- GRIMWOLD, G. H. ('33) Fish meal as a food for clothes moths. *Journ. Econ. Entom.*, vol. 26, pp. 710-712.
- VON IHERING, R. ('14) As traças que vivem sobre a preguiça. *Bradypophila garbei* n. gen. n. sp. *Rev. Mus. Paulista*, vol. 9, pp. 123-127.
- ILLINGWORTH, J. F. ('17) Webbing clothes moth predaceous. *Proc. Hawaiian Entom. Soc.*, vol. 3, p. 274.
- KRA, J. W. ('33) Food-habits of *Timola uterella*. *Florida Ent.*, vol. 17, p. 66.
- SCHULZ, F. N. ('25) Die Verdauung der Raupe der Kleidermotte (*Timus pallionella*). *Biochem. Zeitschr.*, vol. 156, pp. 124-129.
- SITOWSKI, L. ('05) Biologische Beobachtungen über Motten. *Bull. Internat. Acad. Sci. Cracovie*, 1905, pp. 534-548, 1 pl.
- SPULER, A. ('06) Ueber einen parasitisch lebenden Schmetterling, *Bradypodictya babmali* n. sp. *Biol. Centralbl.*, vol. 26, pp. 690-697, 7 figs.
- TURNER, A. J. ('23) A lepidopterous scavenger living in parrots nests. *Trans. Entom. Soc. London*, pp. 170-175.
- WEBSTER, F. M. ('12) The clover mite (*Bryobia pratensis*). *U. S. Dept. Agric. Bur. Entom., Circ.* 158, 5 pp. 3 figs.

#### Change from Phytophagous to Saprophagous Habits

##### 7. Clothes-moths and Fur-moths

- BURGESS, R., and E. J. POOL. ('31) Observations on the susceptibility of animal fibres to damage

##### 8. Wax Moths

- RÖDER, H. ('33) Sind die Wachsmotten Schädlinge? *Entom. Rundsch.*, vol. 49, pp. 32-33; 63- ; vol. 50, pp. 142-144.

- SIEBER, N., and S. METALNIKOW. ('04) Ueber Ernährung und Verdauung der Bienenmotte (*Galleria mellonella*). *Arch. ges. Physiol.*, vol. 102, pp. 269-286.
- DICKMAN, A. ('33) Studies on the waxmoth, *Galleria mellonella*, with particular reference to the digestion of wax by the larvæ. *Journ. Cellul. Comp. Physiol.*, vol. 3, pp. 223-246.
- GÜTZE, G. ('19) Die kleine Wachsmotte (*Achroia grisella* F.) als Samenfresser. *Ann. f. Schädlingsk.*, vol. 5, pp. 97-98.
- KRANCH, O. ('33) Die Wachsmotten sind die ärgsten Schädlinge des Bienenstandes. *Entom. Rundschau*, vol. 50, pp. 140-142.
- KUNICK, G. ('30) Zur Biologie der kleinen Wachsmotte, *Archaea grisella*. *Zeits. angew. Entom.*, vol. 16, pp. 304-316, 25 figs.
- MANUNTA, C. ('33) Sul metabolismo dei grassi nella tignuola degli alveari (*Galleria mellonella*). *Rend. Accad. Lincei, Cl. Sci. fis. mat. nat.* (6), vol. 17, pp. 309-312.
- METALNIKOV, S. ('08). Recherches expérimentales sur les chenilles de *Galleria mellonella*. *Arch. Zool. Expér.* (4), vol. 8, pp. 489-588.
- Change from Parasitic to Phytophagous Habits*
9. *Phytophagous Chalcid-flies*
- CROSBY, C. R. ('09) On certain seed-infesting chalcid-flies. *Bull. Cornell Univ. Agric. Exp. Sta.*, No. 265, pp. 367-388, 2 pls.
- CROSBY, C. R. ('13) A revision of the North American species of *Magastignus* Dalman. *Ann. Entom. Soc. America*, vol. 6, pp. 155-170, 10 figs.
- DOZIER, H. L. ('33) Two important West Indian seed-infesting chalcid wasps. *Journ. Dept. Agric. Puerto Rico*, vol. 16, pp. 103-112, 5 figs.
- GAHAN, A. B. ('22) A list of phytophagous Chalcidoidea with descriptions of two new species. *Proc. Entom. Soc. Washington*, vol. 24, pp. 33-58.
- GRAENicher, S. ('05) On the habits of two ichneumonid parasites of the bee, *Ceratina dupla* Say. *Entom. News*, vol. 16, pp. 43-49.
- HOWARD, L. O. ('96) The grain joint-worm flies and their enemies: A consideration of some North American phytophagous Eurytominae. *Bull. U. S. Dept. Agric., Div. Entom.*, No. 2, pp. 24, 10 figs.
- MARCOVITCH, S. ('15) The biology of the juniper berry insects, with descriptions of new species. *Ann. Entom. Soc. America*, vol. 8, pp. 163-181, 7 pls.
- MAYR, G. ('05) Hymenopterologische Miscellen IV. *Verh. zool.-bot. Gesellsch., Wien*, vol. 55, pp. 529-575.
- MILLER, J. M. ('14) Insect damage to the cones and seeds of Pacific coast conifers. *Bull. U. S. Dept. Agric.*, No. 95, 7 pp., 2 pls.
- NIELEHN, J. C. ('06) Beiträge zur Biologie der Gattung *Cryptocampus*. *Zeitschr. wiss. Insektenbiol.*, vol. 2, pp. 44-47.
- PHILLIPS, W. I., and W. T. EMERY. ('19) A revision of the chalcid-flies of the genus *Harmolita* of America north of Mexico. *Proc. U. S. Nat. Mus.*, vol. 55, pp. 433-471, 10 pls.
- RIMSKY-KORSAKOW, M. ('14) Chalcids of the genus *Isaroma* injurious to grain crops in Russia [In Russian]. *Mém. Bur. Ent. St. Petersburg*, No. 11, 84 pp.
- RIMSKY-KORSAKOW, M. ('23) Phytophage Schlupfwespen als Getreidefeinde. *Suppl. Entomol.*, vol. 9, pp. 16-22.
- ROHWER, S. A. ('12) Chalcidids injurious to forest tree seeds. *Bull. U. S. Dept. Agric. Bur. Entom., Tech. Ser.*, No. 20, pt. 6, pp. 157-163.
- WEBSTER, F. M. ('06) Some insects affecting the production of red clover seed. *Circ. U. S. Bur. Entom.*, No. 69, 9 pp.





# THE PRINCIPLES OF BIOCOENOLOGY

By G. F. GAUSE

*Zoological Institute of the University of Moscow*

THE present review is the exposition of a series of recent investigations in quantitative biocoenology. Its object is to demonstrate certain principles of an experimental approach to the structure of the associations of organisms or biocoenoses. In the study of these associations in the past, investigators laid stress on the morphological side, and scarcely felt the need for applying here an experimental, analytical method. However, it would be as illogical to limit oneself to the morphological investigation of the biocoenosis as to study an aeroplane as though it were an inert and static machine. It is now beginning to be generally recognized that the biocoenosis as a dynamic unit possessing a primitive organization ought to be studied with the aid of the analytical as well as the morphological method.

If a separation of the morphological point of view from the functional one was to a certain extent justified in the past development of cytology, and *idiobiology* in general, there does not seem to be any such justification in modern biocoenology. The laws of form depend here so evidently on the dynamics that any attempt to establish the properties of a structure independently of its transformations is destined to failure. But in our usual observations under natural conditions the complexity of the environment prevents the drawing of reliable conclusions as to the causes of the transformations. Great opportunities are therefore given here to the experimental method, which can be applied *in nature* as well as in the laboratory. The technical possibilities of experimenta-

tion in biocoenology are extremely great. We can directly see how the separate components and elementary processes of the struggle for existence become organized into a whole, and how the laws of form evolve out of the laws of dynamics.

In the present review the mode of approach to the study of organization of the biocoenosis is decidedly an analytical one. At the same time we emphasize the fact that we are only concerned with the principles of organization, and that there remains a great deal of experimental work for their further concretization. The literature on the elementary processes of competition between the components of a biocoenosis has been already summarized by me in *The Struggle for Existence* (1934) and *Vérifications expérimentales de la théorie mathématique de la lutte pour la vie* (1935), and there is no need to repeat it here.

## THE BIOCOENOSIS AS AN ORGANIZED UNIT

1. The recognition of the existence in nature of communities of living organisms or "biocoenoses" probably dates back to the ancient Greeks. In the modern period many botanists endeavored to understand the mutual relations among plants, and the following definition, due to Möbius (1877), is frequently quoted in hydrobiology:

Every oyster bed is in a certain degree a community of living organisms, a combination of species and a population of individuals which find here everything needed for their growth and multiplication. As yet science has no word by which such a community of living beings might be designated, no word for a community where a total of species and individuals is mutually limited and selected under the influence of

average external conditions of life. . . . I propose the word *biocoenosis* for such a community.

The turning point in the history of biocoenology has been the publication of numerous botanical investigations at the close of the last and the beginning of the present century, which demonstrated that the vegetable covering of the earth is divided into natural units of structure or associations. The establishment of a definable unit has automatically led to greater precision of observation and of thought.

If the significance of the biocoenosis as a unit of structure in the living cover of the earth (including animals and plants) does not leave any room for doubt, the degree of organization of this unit is far from being definitely understood. Morphological observations on the structure of biocoenoses show that the latter are characterized by a definite tectological composition and by a definite "texture." In other terms they consist of definite elements in a fixed numerical relation with each other. Elton (1933) remarks, for instance, that the total number of species in an association is a fixed one, and is determined by some important principle. The limitation of the number of species (of which we will become convinced further on) is apparently connected with the limited number of the "ecological niches" which can be utilized by different species without expelling one another, as the number of species saturating the habitat is greater in a more diverse environment. Consequently a biocoenosis consists of only a part of the forms that could potentially enter into its composition. It is already organized in the sense that its membership is a limited one.

The general criterion of an "organized" system is the presence of firmly established relations maintained by regulation and we

will evidently have to decide by means of some kind of dynamic method whether or not this definition holds true for the biocoenosis. *Do there exist any constant characters of constitution and of structure maintained by regulation? In other words, can certain combinations of organisms be stable ones, and the intermediates between them not, even under intermediate conditions?* The solution of this problem can be easily reached with the aid of the analytical method.

A comparison of the organization of a biocoenosis with that of living matter is sometimes made. But such a comparison is scarcely justified at the present time. First of all we have not yet any sufficiently clear understanding of the organization of living matter itself. The underlying units of its constitution are much smaller than those which are revealed by the microscope and scalpel. We can only hope that in the future we shall obtain a better insight into the laws of the molecular organization of living matter. The formation of an organized system on the primitive level of a biocoenosis ought to be therefore considered as an independent and important problem, which at the present time is quite ready for analysis.

2. Let us briefly examine certain observations in field conditions concerning the properties of the biocoenosis as a unit of structure. First of all arises the question whether there exists a sharp spatial separation of one type of structure from another. A number of botanists (Du Rietz, 1921, 1930; Chouard, 1932) give an affirmative answer to this question. In spite of the variety of conditions continuously passing from one value to another only a limited number of distinct associations can be usually established. One complex is sharply separated from another, and the intermediate combinations of species are not observed. However, no unanimity on the subject has been yet

attained (Gleason, 1926) owing to the complexity of field conditions.

To establish objectively how one kind of structure is separated from another an investigation is usually made as to transition of one type of distribution of organisms in space into another. The essential characteristic of the type of distribution in space is relatively simple. We calculate in how far the components of the biocoenosis are distributed in space at random (or not at random), and how sharply a statistical law of distribution peculiar to one association passes into another law in a new association. Regarding many components indications exist that they are not

investigation into  $N$  squares, count the number of individuals of a certain species found on the square ( $v_1$ ) and establish the mean value or abundance ( $v$ ). The statistical investigation shows that if the individuals (or components in general) are distributed according to the law of chance, the square of the standard deviation  $\sigma^2$  (of the variation series constructed with the values  $v_1$ ), divided by the square of abundance ( $v^2$ ) and designated as the relative square mean fluctuation  $\delta^2$  must be equal to the inverse value of abundance  $\frac{1}{v}$ :

$$\delta^2 = \frac{\sigma^2}{v^2} = \frac{1}{v}$$

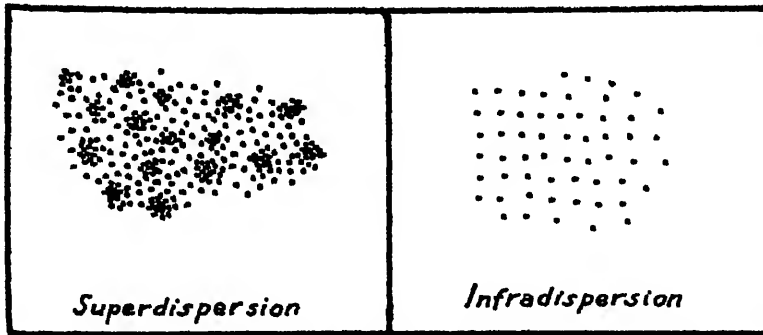


FIG. 1. TWO TYPES OF THE DISTRIBUTION OF ORGANISMS IN SPACE

scattered in the association according to the laws of chance, but are rather grouped into aggregations (Gray and Treloar, 1933; Allee, 1934). Then the character of the statistical distribution of such mosaic complexes or aggregations in the biocoenosis can serve as a criterion of the homogeneity of the latter. If the biocoenosis is homogeneous, the aggregations for their part can be distributed in it according to the laws of chance.

A very accurate method for investigating the character of the spatial distribution of the components in the biocoenosis has been elaborated by The Svedberg (1922). We can divide a plot under

Representing  $\frac{\sigma^2}{v^2}$  as the  $\delta^2$  found, and  $\frac{1}{v}$  as the  $\delta^2$  calculated, it can be said that if the components are distributed at random the ratio  $\delta^2$  found/ $\delta^2$  calculated must be equal to 1. This ratio is called *the coefficient of dispersion*. Every deviation from random distribution in space leads to a deviation from unity of the value of the coefficient of dispersion. Thus, for instance, if the components are distributed in aggregations the per cent of the squares bearing the number of components deviating from the mean value will be greater than we might expect from normal distribution. The  $\delta^2$  found will be greater than

$\frac{1}{v}$  and the coefficient of dispersion will be  $> 1$  (Superdispersion, Fig. 1). But if the components are distributed too regularly (for example the stems of moss when very close together) the coefficient of dispersion will be smaller than the unit (infra-dispersion).

3. The most important structural property of the biocoenosis is the existence of definite quantitative relations between the abundant species and the rarer ones. In this connection let us consider biocoenological terminology. The *abundance* of a species is characterized by the number of individuals on a unit of surface, and the

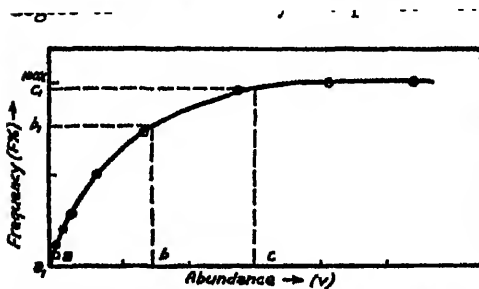


FIG. 2. THE RELATION BETWEEN ABUNDANCE AND FREQUENCY IN THE SNAIL, *VALLONIA PULCHELLA* (According to Beklemishev, 1931)

abundance of a given species in the abundance of the total population. Another characteristic represents the *frequency*, or the per cent of the samples in which the individuals of the given species have been found in proportion to the entire number of the investigated samples. If we have examined a hundred samples and found a definite species in twenty-five of them the frequency will be 25 per cent. Frequency represents a complicated statistical characteristic which depends on abundance, the size of the sample and the type of the distribution of the organisms on the plot. On a plot of large size we will find all the organisms of the biocoenosis and frequency will become simply transformed into a list

of the species. It is very important to bear in mind the connection between frequency and abundance with the constant size of the sample plot. This connection will depend on the character of distribution of the organisms in space. For the simplest case of a normal dispersion frequency will be an exponential function of abundance:  $F\% = 100(1 - e^{-v})\%$ , where  $F\%$  is frequency and  $v$  abundance. Figure 2 represents this relation often encountered in practice (Beklemishev, 1931; McGinnies, 1934). With the increase of abundance frequency approaches gradually to 100 per cent on the typical saturation curve.

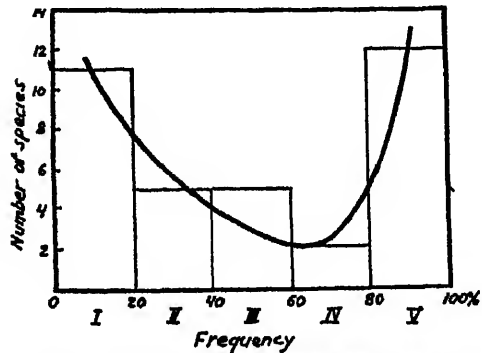


FIG. 3. A TYPICAL CURVE FOR THE DISTRIBUTION OF FREQUENCIES (According to Du Rietz, 1921)

In spite of the great complexity of such a characteristic as frequency many authors have often used it in the investigation of the structure of associations. With a certain moderate size of the sample plot (upon which the frequency of only the most abundant species attains 100 per cent and in others is still very low) we can group frequencies into, for instance, 5 classes: 0-20, 20-40, 40-60, 60-80, 80-100 per cent and determine the number of species which belong to each of them. Jaccard (1902) was the first to build such curves, and Raunkiaer established the following law (Raunkiaer, 1918; Kenoyer,



1927; Gleason, 1929): the greatest number of species belongs to class 0-20 per cent, i.e. they are rare. As the order of the class of frequency rises the number of species belonging to it decreases and reaches a minimum in the fourth class (60-80 per cent) and then rises again in the fifth class (80-100 per cent), attaining a second maximum on the greatest frequencies (Fig. 3). In this manner it becomes possible to separate out of the whole mass of species in the biocoenosis a certain definite group of the most frequent ones which Du Rietz (1921) calls *the constants* of the association. The size of the sample plot upon which these species attain a frequency of 90-100 per cent is called *the minimum area*. In a "real" association, according to Du Rietz, the number of "constant" species (with a frequency of 90-100 per cent) is considerably greater than the number of species in the middle classes of the frequency scale. In artificial "mixtures," on the contrary, it is the great number of species in the middle classes of the scale that is peculiar. In other terms in a "real" (or, evidently, in an "organized") biocoenosis *the predominating part of the biomass belongs to a separated group of frequent or constant species*. This is due to the fact that the organized association is the product of a long process of struggle for existence and of mutual aid. Here survived a few species or combinations of species that are more successfully adapted to particular ecological niches of the habitat and they constitute the basic biomass of the association. There is evidently no such structure in an unorganized mixture. Thus, according to Du Rietz, we can consider the structure of the association as the outcome of a long process of competition and selection.

4. We will soon see that the presence of a definite structure in the biocoenosis may or may not correspond to a state of organi-

zation. One can judge of this latter only by the dynamic and not by the morphological properties. But let us now consider certain difficulties in the work with frequencies. It has been repeatedly pointed out (Gleason, 1929; Romell, 1930) that frequency represents a complicated statistical characteristic, and that in this connection the causes of an accumulation of species in the maximal (fifth) class of frequency require a special analysis. *Does this accumulation reflect the very essence in the structure of the biocoenosis—a certain natural separation of a group of constant species—or is it a statistical artifact?* The possibility of the latter has been mentioned by Gleason (1929). Let us now turn to fig. 2 and suppose that in a certain definite class of abundance, *ab*, fall ten species and that in another analogous class, *bc*, fall also ten species. Taking into account the relation between abundance and frequency it can be easily seen that the first ten species will be dispersed upon a larger section of the frequency scale,  $a_1b_1$ , than the second ten species ( $b_1c_1$ ). In this manner, owing to the exponential relation between abundance and frequency, the most numerous species widely distributed on the scale of abundance can become artificially grouped on a very small section of the scale of frequency. The considerations advanced by Romell (1930) lead also to a notion of the great statistical inclusiveness of the last class of frequency, although his arguments are of a somewhat artificial nature. If we add to this the influence upon frequency of the size of the sample plot and of the character of the dispersion of the organisms in space we will easily come to the following conclusion: *for obtaining an objective representation of the structure of the biocoenosis we must have recourse to some characteristic simpler than frequency.*

The most convenient for this purpose is

the abundance of organisms. In fact it often turns out that the constant species are at the same time the dominant ones, i.e. they predominate as regards abundance (Katz, 1930). Du Rietz (1930) directly introduces the existence of constant dominants in every layer of vegetation into the definition of a phytocoenosis. It is therefore interesting to examine upon existing facts to what extent the group of the most abundant or dominant species is naturally separated in the structure of a biocoenosis. We can analyze the relation between the class of abundance and the number of

the classes of abundance in the lichen stratum of *Pinetum*-association, and curve (2) that of 23 species of plants in the association of *Filipendulatum*. In both cases the sharp separation of two types of species—the abundant and the rarer ones—is quite apparent. The total population is sharply divided into two categories: the numerically dominant species and the non-dominant ones, represented by a small number of individuals. Consequently we arrive here at a conclusion corresponding to that of Du Rietz—the basic biomass of the biocoenosis belongs to a few dominant

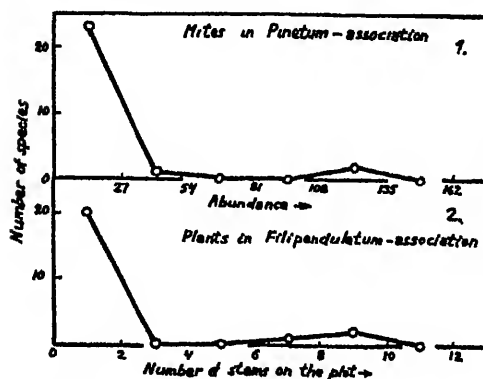


FIG. 4. THE RELATION BETWEEN ABUNDANCE AND THE NUMBER OF SPECIES

(1) Distribution of 26 species of mites. Data from Beklemishev, 1931. (2) Distribution of 23 plants. Data from Beklemishev and Igoshina, 1928.

species belonging to this class. It is often supposed (Gleason, 1929; Beklemishev, 1931) that this relation is of a simple statistical character. In other words the greater the class of abundance the less numerous is the number of species belonging to this class, and in this way no natural separation of a group of abundant species can be observed. However, it is not difficult to see that the situation frequently differs. In Figure 4 are given the curves we have constructed on the basis of the data of Beklemishev and his collaborators (1931). The curve (1) shows the distribution of 26 species of forest mites in

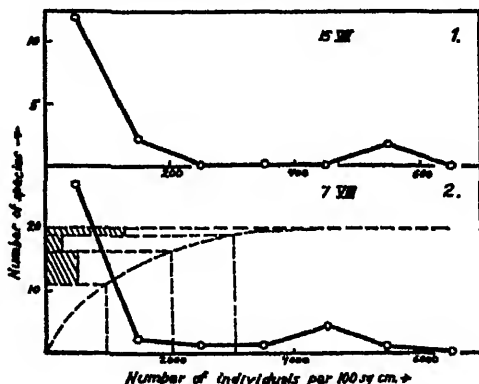


FIG. 5. THE RELATION BETWEEN ABUNDANCE AND FREQUENCY IN THE POPULATING GLASS PLATES SUBMERGED IN THE WATER

(1) young and (2) mature biocoenoses. Data from Duplakov, 1933

species. (For such calculations abundance ought to be expressed in biomass, and not in the number of individuals.)

5. An interesting example from hydrobiology shows that a specific structure can exist in organized as well as in unorganized biocoenosis. Thus Duplakov (1933) following the method of Hentschel (1916) investigated the process of population of glass plates plunged in summer into the water in the shore zone of a lake in Middle Russia. Three days after the beginning of the experiment (15.VII) there was on the glass a typical immature and unstable biocoenosis in which the group of

dominant species was at the same time sharply apparent. On the basis of his data we constructed the curves given in Figure 5. The dominants of the immature biocoenosis were simply the species abundantly represented in the surrounding medium, fixing upon the glass and growing rapidly. Such a feature of an organized state as the regulation of the composition was here entirely lacking. The biocoenosis changed rapidly and only later become somewhat stabilized as regards its qualitative composition. In such a mature biocoenosis (7.VIII) one can also distinguish a group of dominants, but now consisting of species that have shown themselves best adapted to separate ecological niches in the habitat. Figure 5 shows how in the distribution according to the classes of frequency these dominants give a peak in the higher class (dotted diagram). It appears that in working with land vegetation it is more difficult to observe a definite "structure" in unstabilized systems as the process of population is here less regular than in the water of the lake. In this connection botanists use another structural method for recognition of the stabilized biocoenosis (Chouard, 1932). Peculiar to the latter is the presence of a sharply outlined type in the number of species per unit of surface: the variability in the number of species in the sample is represented by the normal variation curve. In the case of unstabilized biocoenoses owing to the irregularity of dispersion there is no sharply outlined typical number of species holding good for the entire territory. The variation curve of the number of species in the sample is irregular and shows several peaks. But in the case of a glass plate being populated in the lake the course of the population is so regular that an immature biocoenosis also possesses a "type." In this way the existence of a definite struc-

ture shows often, *but not always*, a stabilized state of the system. The necessity of a combined morphological (structure) and dynamic (stability) approach to the understanding of organization of biocoenoses is obvious, and it is already recognized by botanists (Du Rietz, 1930).

6. Turning to the structure of stabilized systems we must point out the important principle elaborated by Clements (1916) concerning the very process of stabilization. His observations on vegetation led him to the idea of a gradual development of a stable type of association or *climax* which, owing to its stability, does not allow of any intrusion of new species whereas the unstable intermediate associations admit such an intrusion. The structure of a stabilized system is evidently connected with the fact that some best adapted species have occupied the principal ecological niches. The group of dominants will be the more numerous the greater is the number of different niches or, in other terms, the more the association is "ecologically specialized" (Du Rietz, 1921; Lundbeck, 1926). In a more homogeneous environment the number of dominants falls (Frey, 1927). In any case we can say with certainty that at the basis of the structure of a biocoenosis lies the "niche" structure. The group of rare species is apparently a heterogeneous one and includes the immigrants coming from neighboring habitats, and those individuals that find convenient conditions for living on the various plots existing together with and between the basic niches. The fact of the group of abundant species being usually separated from that of the rarer ones represents a proof of the absence of a continuous transition between the dimensions of the fundamental niches and those of the additional plots. This regularity is especially apparent in the separate layers or *sinusia* of the biocoe-

nosis (Du Rietz, 1930), as the structural properties are here not so much overshadowed by the statistical variability of dimensions of the basic niches.

Summarizing, it can be remarked that the biocoenosis possesses a definite structure whose degree of organization must be investigated experimentally. Field observations raise before us the following problem: How under continuous change of the environment from one value to another can arise stable, spatially separated structures whose composition is maintained by regulation? In other words, how does a state of organization arise?

#### ON THE PRINCIPLES OF ORGANIZATION

1. The simplest way of answering these questions will be to begin an examination of the principles of organization by pointing out that there exist biocoenoses of two types: the *unstable* and the mature or *stable* ones. The process of development leading to stabilization can be particularly well observed on the population of glass plates plunged in natural fresh waters. Recent observations (Ivlev, 1933) show that the process of development of such a biocoenosis falls pretty regularly into two periods: a period of *accumulation* with a simultaneous growth of all the principal components of the biocoenosis, and a later period of reconstruction, when under the influence of competition and of other biocoenotic relations a part of the components is suppressed and begins to diminish in number whilst others develop in even greater abundance (Fig. 6). However, in fresh waters of our latitude a final stabilization of the system is never attained. Having reached a certain stability it continues uninterrupted alteration under the influence of variation of the external medium and finally dies off almost completely in the winter period. It is therefore easy to understand why the idea of

"moving equilibrium" is particularly wide-spread among hydrobiologists (Resvov, 1924).

Recently Duplakov (1933), whom we have already mentioned, carried out a very careful investigation of the process of population of glass plates submerged in Lake Glubokoe (near Moscow), and we

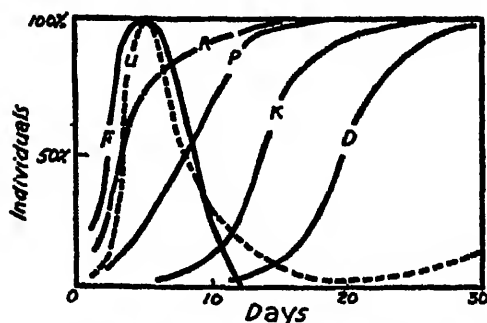


FIG. 6. THE DEVELOPMENT OF POPULATION ON THE GLASS PLATE SUBMERGED IN THE MOSCOW RIVER

F-non-motile Flagellate, U-non-motile Protozoa, R-moving Rotatoria, P-moving Protozoa, K-non-motile Rotatoria, D-Diatomaceae. From Ivlev, 1933.

TABLE 1

The increase of the number of species in a biocoenosis. (Glass plate submerged in Lake Glubokoe.) According to Duplakov, 1933

DAYS AFTER BEGINNING OF THE EXPERIMENT	NUMBER OF SPECIES
1	13*
3	20
5	33
7	33
9	43
26	47
42	45

\* Five of these will disappear on the ninth day.

will discuss here some of the results obtained. Table 1 shows that the number of species in the populating biocoenosis continuously increases after the submersion of the glass plate into the water and attains a certain stability towards the ninth day (43 species). This number remains approximately constant up to the forty-second day. The slight alterations

occur only at the expense of accidental immigrants represented by an insignificant number of individuals. Some of the first settlers soon disappear, but from the ninth to the forty-second day the qualitative composition of the biocoenosis remains almost the same. These data are therefore in accord with the view of Elton (1933) as to the constancy of the number of species in a biocoenosis, which was based upon the macro-components.

Figure 7 represents some typical curves of growth of separate components. After 24 hours of submersion of the plates one can find *Vorticella* upon them. The num-

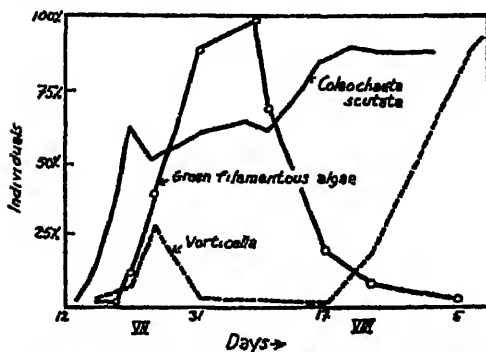


FIG. 7. SOME TYPICAL CURVES OF GROWTH OF SEPARATE COMPONENTS ON THE GLASS PLATE SUBMERGED IN THE WATER

From Duplakov, 1933

ber of these increases very rapidly and reaches a maximum after 12 days. After this the number of *Vorticella* decreases considerably under the influence of the developing filamentous algae (*Oedogonium* and *Spirogyra*), whose growth is intense in the light (whilst in the dark they are incapable of disturbing the animal nature of the biocoenosis). The expulsion of *Vorticella* from the biocoenosis by the filamentous algae can be explained by the fact that an abundant development of the latter prevents the nutrition of *Vorticella*. Indeed, by its mode of nutrition *Vorticella* belongs to the "sedimentators," and requires for the absorption of the sus-

pended nutritive particles a free circulation of the water which surrounds them. The developing flakes of green algae interfere with this circulation. Towards autumn the filamentous algae finishing their cycle die off, and *Vorticella* develops again.

The curves of development of the lamellate green algae (*Coleochaete* and *Stigeoclonium*) are of peculiar interest. In Figure 7 is traced the curve of growth of a number of individuals of *Coleochaete scutata*. Soon after the beginning of the experiment numerous germinating algae settle down on the glass plate and begin to develop into small lamellae. Later the increase of the number of the lamellae ceases owing to a lack of room. The larger lamellae push off or cover over the young growing algae which have settled on the glass. The overgrowth of the glass by the filamentous algae is also an obstacle to their development. However, at the moment of the strong dying off of the filamentous algae and of another species—*Coleochaete soluta*—owing to seasonal causes, the species *Coleochaete scutata* increases very rapidly, taking possession of the liberated places, and later remains at a new fixed level.

It can be said with perfect assurance that the biocoenosis is subject to regular development and attains a certain state of stability which, however, is very strongly altered by the seasonal variation in the lake. The main factors of development are the biocoenotic relations between organisms—competition, destruction and mutual aid—and if there were no seasonal changes these would be the only factors of development. The type of the external medium defines the relative advantage of some components over others and, consequently, the type of development itself, but this type is realized only by means of the biocoenotic forces (in the case of constant external

conditions). In the associations of large terrestrial plants the rôle of seasonal variations is not so profound, and it is therefore possible to observe distinctly the stability of the final states or climaxes (Phillips, 1934). The possession of organization and of regulations is usually connected only with these final states and these categories consequently represent an outcome of the process of regular development.

2. If the organization is the outcome of development we must evidently establish the factors governing the dynamics of development and express them in the form of differential equations. The solutions of these equations will indicate the stationary states and furnish complete information about the regulation of these states. The experiments made under constant laboratory conditions can easily verify the theoretical conclusions. We can also analyze the influence of the external factors on the stationary states of the system. To what extent do the properties of the system fail to change in proportion to external alterations or, in other words, why are intermediate combinations of organisms impossible under intermediate conditions? How far do the properties of the system change in an abrupt manner with the threshold values of external factors, etc.?

For the details of these calculations the reader is referred to the two books by Gause (1934, 1935) and the paper by Gause and Witt (1935); we will only briefly examine here some of the fundamental principles. The dynamics of development of a biocoenosis resulting from interaction between species can lead, for example in the simplest case of two components, either (1) to a complete expulsion of one component by the other,

associations in the same ecological niche and on the consequent expulsion of some components by others may be found in Nicol (1934). He writes: "M. Beijerinck's view of the condition of associations of bacteria responsible for the production of commercial preparations of soured milk may be expressed by saying that these associations are in unstable equilibrium. On account of this instability it is not possible to continue inoculation of fresh milk from a properly soured sample indefinitely; after a very few transfers the balance has been so much disturbed that an undesirable product results from fermentation. Commercial quantities of yoghurt are therefore made from continually renewed mixtures of the single species, which are maintained in pure cultures in milk."

or else (2) to a *stabilization*, that is to the establishment of a stable combination of the two components. Both theory and experiment show that a complete expulsion of the less adapted species by the better adapted one can only take place in the case of two species belonging to the same ecological niche in the habitat. The stabilization which interests us more immediately can take place in the case of each of the species possessing an advantage in its own ecological niche (a "two-niches" stabilization) or in the case of a mutual (or a one-sided) help between the species (symbiotic stabilization). If we write a theoretical equation of the interaction between the species in such a case we will come to the following conclusion. The process of interaction between the first species ( $N_1$ ) and the second ( $N_2$ ) will lead to a stable mixed population which will be dynamically maintained. This can be easily seen on the graph with  $N_1$  plotted on the abscissae and  $N_2$  on the ordinates (Fig. 8). This stable population ( $A$ ) will represent a "knot" as the mathematicians call it. In other words all the curves of the interaction between species will meet in this point. If we begin with small concentrations of both species ( $a$ ) they will increase until reaching "stable" values ( $A$ ). If we now destroy the equilibrium artificially by

In addition to the experiments mentioned by Gause (1934) interesting data on the instability of microbic

introducing more  $N_2$  than necessary and less  $N_1$  than is necessary for equilibrium ( $a_1$ ), the "stable" combination ( $A$ ) will be automatically recovered. In this manner the mathematical theory shows quite clearly *how the regulation of a type (or of a stable combination) can result from the interaction between species.*

Theoretical considerations of this kind are to a certain extent confirmed by the experimental work. The stable combination of species and its regulation can be observed in a mixed population of two infusoria one of which, *Paramecium aurelia* ( $N_2$ ), utilizes more actively the bacterial

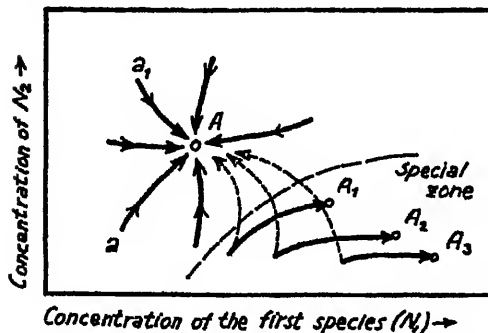


FIG. 8. THE BEHAVIOR OF A MIXED POPULATION OF TWO SPECIES BELONGING TO DIFFERENT ECOLOGICAL NICHES

The dotted lines show the direction of the curves of interaction in the absence of a "special zone."

components of the mixed diet suspended in the upper layer of the liquid, whilst the other, *Paramecium bursaria* ( $N_1$ ) utilizes more actively the yeast settling on the bottom, although both infusoria can live in the entire territory of the microcosm (Gause, 1935). At the same time experimental work points to a certain limitation in the regulation of the typical combination of two species. This regulation is not possible from *all* the points on the surface  $N_1$ ,  $N_2$ . If we bring the population into a "special zone" (Fig. 8) where a new factor not taken into account before is in operation (a peculiar sensitivity of  $N_2$  to the metabolic products of  $N_1$  and

$N_2$ ), the "stable" combination ( $A$ ) cannot become reestablished and we will obtain  $A_1$ ,  $A_2$ ,  $A_3$ , etc. It is easy to show what are here the alterations in the equation of the interaction between species (Gause and Witt, 1935). Observations of this kind are well known to ecologists. In the population of glass plates, for instance, it may be observed that certain forms enter into a "young biocoenosis" and occupy in it a corresponding place ( $N_2$  enters readily when  $N_1$  is not numerous), but can scarcely enter into an "older biocoenosis" (a great deal of  $N_1$ ), as Karsinkin (1936, in press) remarks. This can also be compared to the facts of an incomplete regeneration of climaxes in the plant associations (Ilinsky and Pozelsky, 1929). Usually certain species cannot regain possession of the places that they occupied before.

3. We can conclude that the first feature of an organized biocoenosis—the regulation (within certain limits) of a stable combination of species—can be successfully observed in an experimental way and accounted for theoretically with the aid of a differential equation. The meaning of a regulation in the case of two species belonging to different ecological niches consists in their expelling one another into the zones of maximal effectiveness, so that every disturbance of such a stationary state leads automatically, owing to competition, to the reestablishment of the stable proportion. Such a regulation can take place also in the case of a symbiosis, when with definite relations between the concentrations of the species the greatest advantage for them is attained (see Gause and Witt, 1935). Let us now consider the second feature of the biocoenosis as an organized unit. Many authors have pointed to the fact that with an uninterrupted change of external factors the types of stable combinations of organ-

isms pass abruptly from one to another or, in other words, that the intermediate combinations of organisms are impossible under intermediate conditions. It seems that this important principle can also be theoretically and experimentally demonstrated with simple biocoenosis.

The idea of a theoretical demonstration represents an application of the mathematical conceptions of Poincaré concerning the *change of stability* in a system. If we assume that a definite biological system is under the influence of the temperature gradient which modifies the relations between the fitness of the species, the calculation will show that at fixed moments the system will undergo *qualitative* changes. One type of stable combination will be succeeded by another type of stable combination. The technical details of such calculations can be found in Gause and Witt (1935). Here we can only note that the changes in question are the result of purely biocoenotic causes: after a certain threshold some components cannot withstand the competition but at the same time continue to exist as pure populations. However, under complex natural environment we have to take into account two factors participating in formation of types: (1) biocoenotic, and (2) physiological factors, i.e. the falling out of components in passing their physiological thresholds which takes place both in pure and in mixed populations. These two groups of factors are often closely interwoven and we will now analyze them on a concrete example.

4. Let us consider briefly the results of several new experiments of the author with artificial biocoenoses of Protozoa in order to illustrate the possibilities of the experimental method here. In these experiments a study was made of the influence of a gradual change in a factor of the external medium (hydrogen ion concen-

tration, *pH*) on the formation of the biocoenoses. An attempt was made to answer the two following questions: (1) What are the differences in structure between the unstabilized and the stabilized biocoenoses?, and (2) How sharp is the separation of one type of biocoenosis from another under such conditions?

The experiments were made in tubes for centrifugation with 5 c.c. of the liquid of the following composition: To one liter of twice distilled water add 40 mg. CaO (in boiling water), pass through CO<sub>2</sub> until dissolved, and then add MgSO<sub>4</sub> (5%)—0.5 c.c., Ca(NO<sub>3</sub>)<sub>2</sub> (1%)—0.5 c.c., K<sub>2</sub>HPO<sub>4</sub> (1%)—0.5 c.c., and FeSO<sub>4</sub>—2 mg. to one liter. This medium is favorable to the majority of the Protozoa and its *pH*

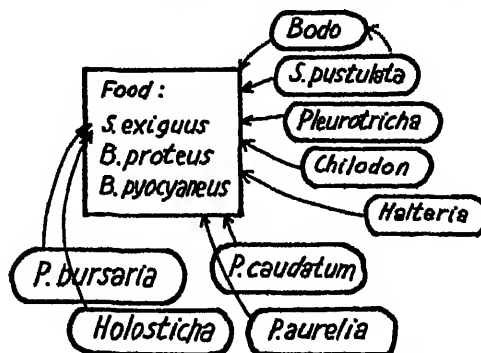


FIG. 9. THE FOOD-CHAIN IN THE EXPERIMENTAL BIOCOENOSIS OF PROTOZOA

is close to 7.9. For a gradual acidulation was used m/10 KH<sub>2</sub>PO<sub>4</sub> and the following *pH*'s were established in separate cultures: 7.6; 7.3; 7.0; 6.6; 6.3. The experiments were made in a thermostat at 24.5°C. with an artificial light according to Hartmann (300 watt). Every day a centrifugation and a change of the medium were made, and likewise the number of individuals in 0.5 c.c. was counted. After the counting the protists were put back into the culture and thus there was no rarefaction of the population. The food consisted of three species of microorganisms which were taken off a solid medium by means of a platinum loop and shaken up in the salt solution. To 30 c.c. was added one loop of *Saccharomyces exiguus*, half-loop of *Bacillus proteus* and half-loop of *B. pyocyaneus*.

Figure 9 shows the food-chain of our biocoenosis consisting of nine species of



TABLE 2

Growth of the number of individuals in experimental bioconozes under different pH of the medium  
(Number in 5 cc.)

DAYS	pH	<i>Paramecium caudatum</i> 0.5 cc.	<i>P. aurelia</i> 0.5 cc.	<i>P. bursaria</i> 0.5 cc.	<i>Stylonychia pustulosa</i> 0.5 cc.	<i>Planorina grandis</i> 0.5 cc.	<i>Helicostoma sp.</i> 0.5 cc.	<i>Halobaea grandinella</i> 0.5 cc.	<i>Chilodon caullerius</i> 0.01 cc.	<i>Bodo sp.</i> 0.01 cc.
0	7.9	6	6	6	5	3	2	3	3	10
	7.6	6	6	6	5	3	2	3	3	10
	7.3	6	6	6	5	3	2	3	3	10
	7.0	6	6	6	5	3	2	3	3	10
	6.6	6	6	6	5	3	2	3	3	10
	6.3	6	6	6	5	3	2	3	3	10
1	7.9	1				2	1	1		
	7.6	4	3		1			2		
	7.3	1	1					1		
	7.0	1	1	1	1			1		
	6.6	1	4		1			1		
	6.3	3						2		
2	7.9	1	1	1	1	1		10		
	7.6	1	1			3	1	7		
	7.3	2	2			2		6		
	7.0	1	5	1		6		8		
	6.6	3				4		12		
	6.3	1	5	2			1	3		
4	7.9		3			7		37		47
	7.6	1	2	2	1	15		7		120
	7.3	3	1	1		14		21		40
	7.0	1	3	5		15		40		24
	6.6	1	5	7		10		68		40
	6.3	7	2	14		2		24		62
6	7.9		4	1	1	9	5	50		22
	7.6	1	2	2		22		30		12
	7.3	2	6	8	1	24		34		16
	7.0	1	9	11	2	15		46		12
	6.6	1	4	13	2	6		80		10
	6.3	1	10	16	2	4		24		8
7	7.9	1	6	3		22	5	100		24
	7.6	2	2	8		16		55	0.5	12
	7.3	1	4	16	1	24		90		8
	7.0	1	7	10	1	9		60		5
	6.6	2	5	8	3	11		95		5
	6.3	4	9	19	4	3		40		6
8	7.9		2	1		9	11	240		26
	7.6			14	1	30		230		44
	7.3	2	3	25	6	8		140		16
	7.0		3	10	1	10		120		6
	6.6	3	7	11	3	7		150		30
	6.3	1	8	24	4	2		90		10
DAYS	pH	<i>Paramecium caudatum</i> 0.5 cc.	<i>P. aurelia</i> 0.5 cc.	<i>P. bursaria</i> 0.5 cc.	<i>Stylonychia pustulosa</i> 0.5 cc.	<i>Planorina grandis</i> 0.5 cc.	<i>Helicostoma sp.</i> 0.5 cc.	<i>Halobaea grandinella</i> 0.5 cc.	<i>Chilodon caullerius</i> 0.01 cc.	<i>Bodo sp.</i> 0.01 cc.
9	7.9									
	7.6									
	7.3									
	7.0									
	6.6	1	7	10	1	8		180	1	7
	6.3	3	14	27	4	5		80		60
10	7.9		8	4	4	3		88		22
	7.6		3	31	1	20		240	1	3
	7.3	1	9	38	7	10		300		4
	7.0		10	32	1	8		144	1	8
	6.6	1	5	26	1	8		240		8
	6.3	2	10	30	3	3		60		11
12	7.9		10	1	2	6		88		6
	7.6	3	8	36	1	10		300		6
	7.3	2	8	40	3	8		230		4
	7.0	1	7	40	3	4		140	1	3
	6.6	1	12	37	7	7		230		9
	6.3	3	16	47	6	5		44		12
14	7.9		8	4	13			120		4
	7.6	1	4	70	3	8		120	1	3
	7.3		12	58	3	6		110		3
	7.0	3	10	37	2	12		120	1	4
	6.6	1	6	37	2	16		125		18
	6.3	2	14	52	12	4		44		8
15	7.9		5	1	8	4		240		8
	7.6		3	58	5	8		80		4
	7.3		16	70	4	8		100		6
	7.0	2	3	70	2	4		110		8
	6.6		8	62	3	10		100		16
	6.3	3	12	66	4			88		5
16	7.9		2	2	8	8		220		9
	7.6		10	80	3	13		60		5
	7.3		13	68	5	8		88		6
	7.0		4	75	2	14		84		12
	6.6		8	70	3	10		105		12
	6.3	2	12	90	5	4		102		6

Protozoa. As a prototype for this biocoenosis was taken an association really existing in nature. It was merely somewhat simplified by a reduction of the number of components, and an important new condition was introduced: the nutritive and physico-chemical properties of the microcosm were maintained at a fixed level. The mean absolute results of the experiments are presented in Table 2, which shows the growth in the number of individuals under different conditions.

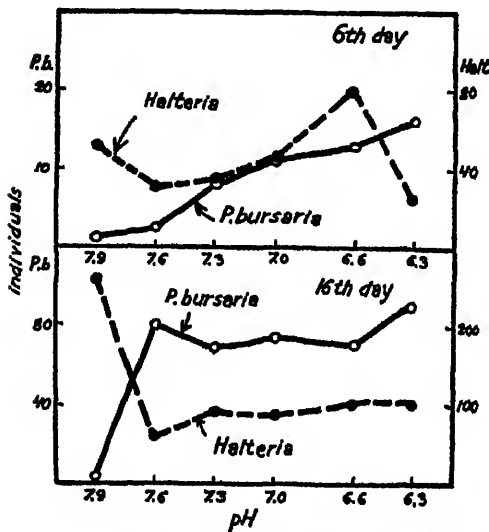


FIG. 10. THE RELATION OF SPECIES TO pH OF THE MEDIUM IN A YOUNG (SIXTH DAY) AND AN OLD (SIXTEENTH DAY) BIOCOENOSIS

An examination of Table 2 enables us to conclude that in a young immature biocoenoses (fourth and sixth days) there is no sharp separation into individualized types at different pH, and the differences between the types are continuous. This is illustrated by Figure 10 which shows that on the sixth day the densities of *P. bursaria* and of *Halteria* do not form any distinct types on the pH scale, and that no sharp differences exist between "phosphateless" and "phosphate" cultures. An entirely different picture is to be seen

in mature biocoenoses (sixteenth day). They are separated into two sharply individualized types—the phosphateless ( $pH = 7.9$ ) and the phosphate ones. A very strong increase in the concentration of the latter scarcely alters the type of the biocoenosis. Thus we have evidence of the formation of individualized units resulting from the process of development.

Turning to a more detailed analysis of the results we must point out that  $KH_2PO_4$  together with a change of pH exhibits an additional specific effect on the protozoa (Beers, 1933 and Gause, 1934). In our experiments there took place a strong depression of *Holosticha* by the phosphate

TABLE 3

The separate growth of population of *Paramecium bursaria* under different pH of the medium. Number of individuals in 0.5 cc. Food: *S. exiguus*

DAYS	pH					
	7.9	7.6	7.3	7.0	6.6	6.3
2	9.5	8	8	9	10	11
4	19.5	14	13	17	18	24
5	41	35	46	54	41	40
6	67	58	44	60	50	51
7	86	70	80	70	61	86

(through not an immediate destruction, as *Holosticha* has been registered on the second day of growth). This depression is already quite distinct in the immature biocoenosis, and is therefore of a physiological and not of a biocoenotic nature. With the further development of the biocoenosis the place of *Holosticha* is taken by *P. bursaria*, which later begins to crowd out *Halteria* and is responsible for a sharp leap in the changes of concentration of the latter as regards pH, which did not exist before. We can say with certainty that the insufficient development of *P. bursaria* in a phosphateless biocoenosis ( $pH = 7.9$ ) is due to the presence of *Holosticha* for, when growing separately,

*P. bursaria* develops in almost the same way in a phosphateless and in a phosphate medium (Table 3). In this way *Holosticha* falls out owing to physiological causes and lets *P. bursaria* into the biocoenosis on one side of the ecological scale, while on another section *P. bursaria* is pushed out (or, more exactly, not admitted) biocoenotically by *Holosticha*. The differences between the types of biocoenoses appear as a result of a complicated interweaving of biocoenotic and of physiological causes, and the stable types themselves change abruptly.

TABLE 4  
Calculations of the volumes of species

SPECIES	LENGTH IN DIVISIONS OF THE OCULAR- MICRO- METER	VOLUME ( <i>P. caudatum</i> = 1)
1. <i>Paramecium caudatum</i> .....		1
2. <i>P. aurelia</i> .....		0.396
3. <i>P. bursaria</i> .....	39.9	0.405
4. <i>Halteria grandinella</i> .....	9.8	0.036
5. <i>Planorhiza grandis</i> .....	32	0.101
6. <i>Gibbidium cucullatus</i> .....	14.5	0.016
7. <i>Bodo</i> .....	2.25	0.00043
8. <i>Stylonychia pustulata</i> .....	63.6	0.770
9. <i>Holosticha</i> .....	30.3	0.098

In order to obtain an idea on distribution of the biomass between the separate species at different stages of growth of the biocoenosis we measured the species under the microscope and calculated their volumes (Table 4). These data have only the character of a very first approximation to the biomasses, as with differences of shape in the species a calculation of their volumes cannot be a very exact one. With the aid of these coefficients we can see that the surplus of biomass of *P. bursaria* in the biocoenosis with  $pH = 7.6$  as compared to  $pH = 7.9$  coincides almost completely with the deficiency in the biomass of *Holosticha* and *Halteria*. If we

take the mean data for the fifteenth and sixteenth day we obtain: (1) an excess of *P. bursaria*:  $67.5 \times 0.405 = 27.3$  and (2) a deficiency of *Holosticha* and *Halteria*:  $230 \times 0.098 + 235 \times 0.036 = 30.95$ . Therefore from the view-point of biomass these components mutually replace one another. An exact coincidence is hardly to be expected here owing to the approximate calculation of the volumes and the differences in productivity of formation of the biomass by different species at the expense of the same food material (Gause, 1934).

TABLE 5  
Distribution of biomass between different species in the experimental biocoenosis on the sixth and sixteenth days of growth.  $pH = 7.9$

SPECIES	VOLUME PER 0.5 CC.	
	6th day	16th day
<i>P. aurelia</i> .....	1.58	0.79
<i>P. bursaria</i> .....	0.40	0.81
<i>Stylonychia</i> .....	0.77	6.16
<i>Planorhiza</i> .....	0.91	0.81
<i>Holosticha</i> .....	0.49	21.55
<i>Halteria</i> .....	1.80	9.37
<i>Bodo</i> .....	0.47	0.19

If we turn now to the distribution of biomass between the different species (Table 5) we will be able to note a certain difference between the immature and mature biocoenoses. In a young biocoenosis (sixth day) there are, as biocoenologists say, no "constants" in the association, that is no natural separation of the group of abundant species from the rarer ones. But such a separation appears on the sixteenth day when we have a group of rare species (0.79; 0.81; 0.81; 0.19) and of abundant species occupying the fundamental ecological niches (6.16; 21.55; 9.37). Therefore one can succeed in observing under experimental conditions the appearance of the structural properties of the biocoenosis which are usually men-

tioned in field observations. We can only remark that such a structural property is not always proof of the maturity and stability of the system. We have already had an occasion to point out that in the population of glass plates in the lake there is a very abundant fixation (and growth) of the components which will not be able afterwards to survive in the competition, and thus a structure may arise even in an immature system.

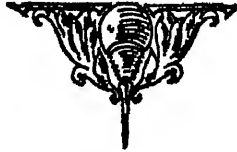
We can endeavor to summarize briefly

our review by pointing out that the fundamental problems raised by field investigations—the regulation of a stable combination of species and the separation of the biocoenoses into individualized natural constructive unities or types in spite of an uninterrupted change in the external conditions—can be successfully analyzed with the aid of the experimental method. The great potentialities of this method for the future of biocoenology admit of no doubt.

#### LIST OF LITERATURE

- (1) ALLEE, W. C. (1934). Concerning the organization of marine coastal communities. *Ecol. Monogr.*, 4, p. 541.
- (2) БРЕКЛЕВИЧЕВ, W. N. (1931). Über die Anwendung einiger Grundbegriffe der Biocoenologie auf tierische Komponente der Festlandbiocoenosen. *Bull. Plant. Protect.*, 1, p. 277 (in Russian).
- (3) БРЕКЛЕВИЧЕВ, W. N., und K. IGOSHINA. (1928). Untersuchungen über die Verteilung von Individuen verschiedener Ordnung in den Assoziationsflecken. *Trans. Biol. Instit. Perm Univ.*, 1, p. 171 (in Russian).
- (4) CHOUARD, P. (1932). Associations végétales des forêts de la vallée de l'Apuance. Application de la méthode statistique à l'étude des groupements de plantes. *Bull. soc. bot. France*, 79, p. 617.
- (5) CLEMENTS, F. E. (1916). Plant Succession. *Corn. Inst. Wash.*, 242.
- (6) ДУПЛАКОВ, S. N. (1933). Materialien zur Erforschung des Periphytons. *Arch. Limnol. Stat. Karsino*, 16, p. 5 (in Russian).
- (7) DU RUIZ, G. E. (1921). Zur methodologischen Grundlage der modernen Pflanzensoziologie. *Upsala*.
- (8) DU RUIZ, G. E. (1930). Vegetationsforschung auf soziationsanalytischer Grundlage. *Abderb. Handb. biol. Arbeitsmeth.*, LX, 5, p. 1.
- (9) ELTON, CH. (1933). The Ecology of Animals. *London*.
- (10) FREY, A. (1927). Le graphique dans la phytosociologie. *Rev. gén. de bot.*, 39, p. 533.
- (11) GAURE, G. F. (1934). The Struggle for Existence. *Baltimore*: Williams & Wilkins.
- (12) GAURE, G. F. (1935). Vérifications expérimentales de la théorie mathématique de la lutte pour la vie. *Paris*: Hermann (Actualités Scientifiques, Exposés de Biométrie).
- (13) GAURE, G. F., and A. A. WITT (1935). Behavior of mixed populations and the problem of natural selection. *Amer. Natur.*, 69, p. 596.
- (14) GLEASON, H. A. (1926). The individualistic concept of the plant association. *Bull. Torrey Bot. Club*, 53, p. 7.
- (15) GLEASON, H. A. (1929). The significance of the Raunkiaer law of frequency. *Ecol.*, 10, p. 406.
- (16) GRAY, H. B., and TRELOAR, A. B. (1933). On the enumeration of insect populations by the method of net collections. *Ecol.*, 14, p. 356.
- (17) HENTSCHEL, E. (1916). Biologische Untersuchungen über den tierischen und pflanzlichen Bewuchs im Hamburger Hafen. *Mitt. Zool. Mus. Hamb.*, 33.
- (18) ILINSKY, A., and POZELSKY, M. (1929). Zur Frage der Assoziierung bei Pflanzen. *Transact. Applied Botany and Selection*, 20, p. 459 (in Russian).
- (19) IVLEV, V. S. (1933). Ein Versuch zur experimentellen Erforschung der Ökologie der Wasserbiocoenosen. *Arch. f. Hydrobiol.*, 25, p. 177.
- (20) JACCARD, P. (1902). Lois de distribution florale dans la zone alpine. *Bull. soc. Vaud. Sci. Nat. (Lausanne)*, 38.
- (21) KATZ, N. J. (1930). Die grundlegenden Gesetzmäßigkeiten der Vegetation und der Begriff der Assoziation. *Beitr. Biol. Pflanz.*, 18, p. 305.
- (22) KENoyer, L. A. (1927). A study of the Raunkiaer law of frequency. *Ecol.*, 8, p. 341.
- (23) LUNDBECK, J. (1926). Die Bodentierwelt norddeutscher Seen. *Arch. Hydrob.*, Suppl. Bd. 7, p. 1.

- (24) MCGINNIS, W. G. (1934). The relation between frequency index and abundance as applied to plant populations in a semiarid region. *Ecology*, 15, p. 263.
- (25) MÖBIUS, K. (1877). Die Auster und die Austerwirtschaft. *Berlin*.
- (26) NICOL, H. (1934). Microbes in association. *Sci. Progr.*, 29, p. 236.
- (27) PHILLIPS, J. (1934). Succession, development, the climax, and the complex organism: an analysis of concepts. Part I. *J. Ecol.*, 22, p. 554.
- (28) RAUNKIAER, C. (1918). Recherches statistiques sur les formations végétales. K. Danske Vid. Selsk. Biol. Meddel., 1.
- (29) RASVOY, P. (1924). On the definition of the biocoenosis. *Russ. Hydrobiol. Journ.*, 3, p. 8 (in Russian).
- (30) ROMELL, L. G. (1930). Comments on Raunkiaer's and similar methods of vegetation analysis and the "law of frequency." *Ecol.*, 11, p. 589.
- (31) SVEDBERG, THE. (1922). Ett bidrag till de statistiska metodernas, användning inom växtbiologien. *Svensk. Bot. Tidskrift*, 16, p. 1.
- (32) THIENEMANN, A. (1925). Der See als Lebensseinheit. *Naturwiss.*, 13, p. 27.



---



---

## NEW BIOLOGICAL BOOKS

*The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.*

### A NOTABLE CONTRIBUTION TO ENTOMOLOGY

Being a review of *A Cluster of Bees* by Tarlton Rayment, Sydney (The Endeavor Press), 1935. 752 pp., 66 plates, 100 text-figures.

By William Morton Wheeler, Harvard University.

Those who believe that the sturdy breed of naturalists is all but extinct and is being supplanted by academic biologists need to revise their opinion by reading the impressive volume on the bees of Australia by Tarlton Rayment, the most recent and the most catholic of the long series of naturalists who have devoted themselves to a study of the Hymenoptera, from prose-poets like Maeterlinck, Everard, Tickner Edwards and behaviorists and ecologists like Réaumur, the Hubers, Fabre, Ferton, von Buttel-Reepen, the Peckhams, the Raus, Hoffer, W. Wagner, Lie-Pettersen, Sladen, Plath, Frison, F. X. Williams, Hingston, Adlerz, Nielsen, Maidl and Grandi to taxonomists like Forel, Emery, Friese and Bequaert. To compare Rayment with any of the living members of this galaxy would be invidious, but a comparison is permissible with Fabre, of whom he says: "I admire the genius of the man; his charming poetry; his devotion to truth; his engaging simplicity; I am pleased to call him 'master'." But while Fabre has always been justly admired as an extraordinary observer and stylist, he suffered from four regrettable infirmities, which have diminished the importance of his works in the

eyes of present day entomologists: he rejected evolution; his conception of insect behavior was essentially medieval and scholastic; he despised taxonomy; he was a constitutional recluse and introvert, and therefore unable to adopt the social and co-operative rôle of the true scientist. Rayment's attitude towards his subject and his fellows is so different that it merits special comment. Though primarily interested in the behavior of the solitary and social bees, he rightly treats morphology and taxonomy as the basis and framework of his investigations. His views on evolution, insect "intelligence" and the importance of cooperation among scientists may be gleaned from the following quotations chosen at random (pp. 253, 189, 164):

"This outcropping here and there of certain specific anatomical developments, as though to demonstrate their common origin, has a parallel in the behavior of the creatures. Evolution is silently directing all life; not only the physical features, but also the mental qualities, are slowly but constantly changing. To deny the discernment of the lower animals, and to assert that bees are only 'reflex machines' is utterly unscientific, for such a contention endeavors to limit the processes of evolution to mere morphological structure and entirely overlooks the fact that brain functions, but that functioning has limits imposed by the evolutionary level already attained."

"In some cases I prefer the thin, sharp point of Wheeler's thrust to the heavy broad-axe of the august Fabre—"It is with this gibberish about continuous flashes of reason that men pretend to build up science today!" Ah, master, I regret that blow!

"Every day I see flashes of reason light up the eyes of my retriever dog. Why, as I write, my fire burns low.

"Brown!" I call sharply; he comes in from the kitchen, stretching himself lazily.

"Bring in some wood!"

He lifts his long ears a little, and cocks his head to one side; his eyes speak as clearly as our own. His whole countenance suggests inquiry.

"A piece of wood!" He did not hear aright. I repeat the command in imperative tone.

"His face relaxes, he wags his feathered tail sharply and departs on the errand.—A minute or two later he returns with a heavy mallee-root, that being the fuel I prefer for winter burning. Moreover, he is proud of his comprehension and ability to carry out the task to which he has been assigned.

"Do I believe animals have intelligence?"

To which I reply: "Nature, having once evolved a muscle, a bone, or a sinew for a certain function, never duplicates the organ. The horse, the sheep, the dog and man each have a femur-bone to enable them to walk and run, and the horse, the dog, the bee and man each have a brain to direct the essential activities of their lives. True, some animals have longer femora, and so run quicker; other animals have better developed brains, and so think more lucidly. I will not waste your time or mine on those who endeavor to prove that the thigh-bone of the ape is for a different purpose to the thigh-bone of the genus *Homo*, and that the brain of the bee has a different function to that of man."

"One of the most charming aspects of science is the universality of the brotherhood. I have only to request the authorities of the Smithsonian Institute, United States, to let me have a few American bees for study, and forthwith they are despatched; and when I desire a copy of some rare or obscure European publication, why, my esteemed friends and correspondents, Doctors Reinhold Meyer, of Darmstadt, and Walther Horn, of the Berlin Museum, courteously oblige me.

"I say the good will existing among the scientists of all nations is the nearest thing to the Universal Brotherhood of Man that this old world possesses. Indeed, the Director of the Berlin Museum has printed in English, on the cover of every scientific paper issued by his institution, the following beautiful expression by Professor Edgworth David of Sydney: "In the world of Science, all men are brothers." What a contrast to the downright selfishness often preached by the politicians in so many lands!"

Not only does Rayment rival Fabre in his keen and persevering powers of observation but he has been more fortunate than the "Homer of the Insects" in his training and in possessing considerable talent as a draughtsman, as shown by the wealth and accuracy of the illustrations which add so much to the excellence of his exposition. His experience of many years as an observant and thoughtful bee-keeper was a much better preparation for the study of the native bees of Australia than chemistry. Fabre's long occupation with that science was probably detrimental to his later work as an entomologist, since it seems to have led him to adopt a too schematic formulation of insect behavior. Indeed, it may be

doubted whether more than a knowledge of the rudiments of the inorganic sciences is the best preparation for the naturalist as distinguished from the laboratory biologist.

A review of Rayment's volume is difficult, partly because it abounds in so many interesting facts and partly because it may be said to represent a new method of presenting the natural history of a whole fauna. He had the good fortune to take up the study of the Australian bees as a pioneer, with only the very recent, taxonomic contributions of Henry Hacker of Queensland and Professor Cockerell, of the University of Colorado, to serve as an introduction. As he says, "over 100 years of occupation by white people elapsed before a single life-history of a native bee was described" in Australia. And yet the island continent has a rich and, owing to the primitive character of many of its species, a remarkable bee-fauna. He casually mentions in the legend to one of his figures that 130 species of bees were observed to visit the flowers of a single *Eucalyptus* (*E. calophylla*) at his home near Sandringham, Victoria. Embedded in a wealth of morphological and taxonomic details, but easily separable by the general reader, are fascinating accounts of the bees of great interest to the student of comparative behavior, interspersed with brief disquisitions, or "asides," which rest the reader, on the Australian plants, so unforgettably and wondrously beautiful to those who have encountered them in the field; charming glimpses of the sunny Victorian landscape; short studies of the Ichneumonid and other parasites and enemies of the bees; affectionate mention of helpers and boy-friends; revelations of the author's dislike of city life and of the picnickers and bathers that intrude on his observation grounds along the shores of Port Phillip, and good-natured comments on the politicians and philistines, who, however, are much less numerous and verminous in Australia than they are in the United States.

The longer first part of the volume comprises a number of short essays, each devoted to observations on the structure, life-history and behavior of a species of bee or of some other insect. The bees

are arranged in the usual putative evolutionary sequence, beginning with the very primitive Hylacidae (Prosopidae) and ending with the social forms (stingless, bumble and honey bees). The Hylacidae are of unusual interest because they have somewhat similar relations to the higher solitary and social bees as the bull-dog ants (Myrmecidae) to the higher ants and the monotremes and marsupials to the placental mammals. In North America and Europe there are only a few hundred species of the single genus *Hylaeus* (Prosopis), but about half the Australian bee-fauna are Hylacids, belonging to some 15 genera, representatives of all of which have been studied by Rayment. Then follow observations on a number of other primitive solitary bees of the families Colletidae and Andrenidae. Several chapters are devoted to observations on 17 species of *Halictus* (Andrenidae), a cosmopolitan genus, with more than 1000 known species (138 Australian) and of diverse and complicated habits. Although Rayment has devoted an almost unbelievable amount of patient study to these bees and has found that the Australian forms are more primitive than the European in their method of lining their brood cells and in the early disappearance of the overwintering nest-mother, he has been able to elucidate the complete life history of only a few of the species. This is not surprising when we consider that a long series of able European entomologists have held the most diverse views with regard to the number and sequence of annual generations in the same species of *Halictus*. Rayment finds that some of his species closely resemble those investigated by Fabre, but, unfortunately, he fails to correlate his results with those obtained by the more recent students of the *Halicti* in Germany—Friese, Blüthgen, Armbruster, Stöckert, Legewie and, especially, Noll, who in 1931 critically reviewed and clarified the known types of generation-sequence in the European and Chilean species.

The higher solitary bees of Australia belong for the most part to cosmopolitan genera and exhibit only the usual slight specific departures from the typical behavior patterns of their congeners. One

species, *Megachile* (*Hackeriaspis*) *deani*, however, shows a surprising innovation in the materials which it chooses for the confection of its cells. Instead of employing cut pieces of green leaves like its ancestors it has taken to making its cells of wax from bee hives. "It is the trade of the creature that has altered. I would remind you, that the doubly-refined white wax, in the form of 'foundation' has been available only since Johannes Mehring invented his press in 1857. Something more than a mere 'reflex machine' is needed to explain this use of an ultra-modern material by a bee that traces its leaf-cutting ancestors back to the Miocene Period (Florissant Shales of Colorado), and, therefore, long before man was evolved to bring utter chaos to his fellow beings." This case, therefore, may be bracketed with the famous cases of the Kea parrot of New Zealand and the Australian blowfly, which have learned to attack living sheep within very recent times.

Only one of the three groups of social Apoidea, the stingless bees (Meliponinae), is native to Australia. It is a purely tropical group with many species in South and Middle America and several in the Ethiopian and Indomalayan Regions. Rayment records 15 species and subspecies, belonging to the genus *Trigona*, from the warmer parts of Australia and gives us the first comprehensive account of their habits, with illuminating comparisons with the hive bee. There is also a fine chapter on this latter insect. Since there are no Australian bumble-bees, he inserts an account of a European species to fill the gap in the series of social types. Though bumble-bees have been introduced repeatedly into Australia by Rayment and others, they have never survived as they have in New Zealand. He is convinced "that the sole reason for the apparent failure of the bumbles to establish themselves is due to the predatory habits of our birds." The overwintered queens seem to be destroyed by the birds before they can establish their colonies.

One of the most surprising passages in the book is an account of a mysterious honey bee, which Rayment dubs *Apis amigmatica*, in the sparsely settled moun-



tain regions of Victoria, far from the range of the other species of the genus. He and several of his correspondents have seen the small combs of this bee, which are only three to four inches in diameter and depend from the limbs of trees or other supports. Apparently the insect is now so rare or so nearly extinct that he has been unable to secure specimens of it though he figures the combs. Concerning the cells which are intermediate in size between those of two of the known species of honey-bee, he says:

"Do you remember Darwin's prophecy which he made after viewing a certain flower? He said that a specific moth would be found that fertilized the plant. The forecast proved a correct one. The combs of the five species of *Apis* always prompt me to emulate the great man, and after studying the diagrams, you, reader, will feel as I do. The cells of the giant bee of India [*A. dorsata*] measure about four to the lineal inch; those of the hive bee [*A. mellifica*] five to the inch; while the eastern honey-bee [*A. indica*] constructs six to the same measure. Then there is a hiatus, for the next are those of this Australian bee [*A. aenigmatica*], and which measure nine to the inch, and last, the small cells of the Indian flower-bee [*A. ferox*], which builds one more to the lineal measure. I look forward to discovering two new species, whose cells will measure seven and eight to the inch: the sequence will then be unbroken."

Some of the parasitic and other insects, incidentally described by Rayment as he unrolls his remarkable picture of a whole fauna, are quite as interesting as the bees but cannot be adequately reviewed in the space at my disposal. A species of Ichneumonid wasp, however, which copulates with the flowers of orchids in order to ensure their pollination, is too startling to be omitted.

"In January, when the orchids [*Gryllistylis leptochila*] are in their prime, behold, it is not the bees that attract the attention of the observers, but a large, though slender, male wasp, a species distributed over the whole of the Commonwealth and New Zealand, and known to science as *Lissonotus sumipunctatus* Kirby. The creature has a reddish head and thorax, but the abdomen is black with a number of pale spots.

I am invited to see for myself the phenomenon of insects effecting a pseudo-copulation with the flowers. But there is no doubt about their actions; the wasps slide down backwards into the flowers, the organs of generation are extruded, the characteristic movements are performed and the seminal fluid is discharged upon the fleshy fold [of the labellum]. It seems inconceivable, but further investigation, and the dissection of several specimens under the microscope, reveals a marvellous correlation between the claspers of the *androgynus* and the *vagina* of the flower;

there are live sperms in the globule on the tip of the insect's abdomen. Yes, anomalous as it may seem, the sex impulse in the male wasp is excited by the blossom with which it attempts to mate, and in the doing has had glued to its body the pollinia for transportation to another flower.

What obscure laws are responsible for this wonderfully close association? Is the wasp misled by the likeness of bright light on the raised glands of the labellum to the pale abdominal markings of the female, or has the scent of the flower some subtle influence that stirs deeply the sexual instincts of the male? Who knows?

I could go on to relate the absorbing story of another Victorian purple species, the large-tongue orchid, *Gryllistylis subulata*, pollinated by the same wasp, but which has to perform the copulatory action while it is upside-down, but there is no necessity for me to weary you with such additional minutiae."

The first part of Rayment's volume closes with several miscellaneous chapters on the combs and strigils of bees, the neurulation of their wings, a classification of the Apoid superfamily, hints to taxonomists and collectors and a series of excerpts on the life-histories of "exotic," that is, non-Australian bees. The second part is purely taxonomic, comprising descriptions of more than one hundred new species, subspecies and varieties of Australian bees and redescrptions of certain forms insufficiently characterized by their authors. The volume contains an adequate index.

The taxonomic portions of Rayment's work will, of course, interest only the specialist, but the portions in larger type will charm the layman no less than the naturalist, and the latter will place the volume in his library among the classic works of Fabre, Wallace, Bates and Belt. It is hardly necessary to add that the "Cluster of Bees" will be an abiding source of inspiration to future students of entomology. The perusal of such contributions sets one to wondering whether the naturalist may not be after all an artist *manqué* or incompletely developed, and not a genuine "scientist." Undoubtedly the activities of the naturalist are to a considerable degree motivated and sustained by esthetic delight in the wonderful forms and colors of animate beings and the intricate temporal patterns, or configurations of their life-histories, behavior and ecological settings. Unlike the "pure scientist" who is devoted to simplicity, the naturalist like the artist, feels at home in the profusion, multiplicity and diversity

of natural phenomena. Lovejoy, in his "Great Chain of Being" (Harvard Univ. Press, 1936), calls attention to these two types of mind, of which I would cite Pascal and Alexander von Humboldt as striking illustrations, when he says (p. 7): "There is, for example, a practically very important difference between (we have no English term for them) *esprits simplistes*—minds which habitually tend to assume that simple solutions can be found for the problems they deal with—and those habitually sensible of the general complexity of things, or, in the extreme case, the Hamlet-like natures who are oppressed and terrified by the multiplicity of considerations probably pertinent to any situation with which they are confronted and the probable intricacy of their interrelations." There seems to be a significant resemblance between these simplicist and multiplicitist types and the old distinction between Platonists and Aristotelians, between the introverts and extroverts of Jung, the classicists and romanticists of Wilhelm Oswald, the Apollinians and Dionysians of Nietzsche, the tender minded and tough minded individuals of William James, the schizothymes and cyclothymes of Kretschmer, the "idéo-émotifs" and "sentimen-

taux" of Remy de Gourmont, etc. In this connection it may be mentioned that D. C. Peattie's delightful volume, "Green Laurels" (Simon and Schuster, N. Y., 1936) gives an unusually subtle and appreciative insight into the dominant motivation of naturalists.

Perhaps, too, the naturalist's preoccupation with taxonomy has its roots in an unavowed conviction that this "science" is really an art. Nor does his fervid search for truth contradict the foregoing statements, since the artist is quite as much concerned with truth as the scientist, though the naturalist seems to be more desirous of appreciating and understanding than of explaining the phenomena with which he deals. This may account for the non-mathematical and non-experimental spirit in which he approaches and handles his materials. It may also account for his somewhat unsympathetic attitude towards the bright highschool boys now bombinating in the biological laboratories of our universities. He feels that not a few of these neophytes manifest a somewhat gangster attitude towards Nature, so eager are they to assault, scalp or rape her, and so unmindful of the old apothegm, *Natura non vincitur nisi parendo*.

## BRIEF NOTICES

### EVOLUTION

#### EVOLUTION.

By A. Franklin Shull. McGraw-Hill Book Co., New York. \$3.00. 9 x 5½; x + 312; 1936.

This treatise constitutes a general discussion of biologic evolution as interpreted in the light of modern genetic discoveries. The first chapters of the book are given to a clear and detailed presentation of the facts which lead to the concept of evolution; the existence of differences between groups of living creatures, the geographic distribution of species, cytology, genetics, and the known factors of genetic variation. The general conclusions drawn from these facts do not admit of contradiction and form the foundation of modern biology. In the following chapters, which discuss the several theories of natural selection, protective and warning coloration, adaptations,

etc., even though the author struggles to find some consistent explanation of the facts and theories, it is evident that the actual mechanism of evolution, the how, why and where, is yet unknown. The exceptional competence of the author and the excellent review of the wealth of facts and theories at his disposition renders this volume interesting and essential not only for students of biological sciences but also for the layman. Throughout the book the author demonstrates a well balanced critical judgment although, in the reviewer's opinion, the neo-Lamarckian theories deserve more attention, at least from the historical standpoint. At times the author's language lacks preciseness; for example, "If only those things were true which have been proven true there would be little verity in the world." (p. 211.) This sentence, if taken literally, would indicate a disregard for scientific method, which we are sure the author has not.

AM WENDEPUNKT DER STAMMESGESCHICHTE.  
By Carl Theo Kempermann. *Gustav Fischer, Jena.* 1.50 marks.  $9\frac{1}{2} \times 6\frac{1}{4}$ ; 32; 1936 (paper).

The discussion of vitalism and mechanism, although it never comes to any permanently satisfactory conclusion is one that always fascinates biological thinkers. In this pamphlet, the author has arranged the arguments for both sides in compact form. He is thoroughly conversant with the works of Linnaeus, Lamarck, Darwin, Haeckel, Dacqué, Smuts, Haldane and others and presents their theories clearly and briefly. He is rather inclined towards a holistic conception of evolution. The work presents no new approach to the problems of evolution, or of mechanism and vitalism, but is intended only as a survey and guide for students.



#### Происхождение Растения

В. Л. Комаров. Издательство Академии Наук СССР, Ленинград. 3 руб. 50 коп.; 192; 1936.

#### [THE ORIGIN OF PLANTS.

By V. L. Komarov. *Publishing House of the Academy of Sciences of U.S.S.R., Leningrad.* 3.50 roubles (paper), 5 roubles (cloth).  $9 \times 6$ ; 192; 1936].

This little book written by Professor Komarov, member of the Academy of Sciences of U.S.S.R., gives a popular account of the origin of different groups of plants, of their gradual spreading upon terrestrial habitats, and of the evolutionary processes of differentiation of their forms. The style is easy and comprehensible.



#### GENETICS

##### HEREDITY AND EVOLUTION.

By Arthur E. Watkins. *John Murray, London.* 7s. 6d. net.  $7\frac{1}{2} \times 5\frac{1}{8}$ ; viii + 243 + 2 plates; 1935.

In this volume the attitude of genetics towards evolution" is set forth clearly and concisely. It is a book which biological students will find useful, yet it is by no

means too formidable for the general reader. The author (University Lecturer in genetics and cytology, Cambridge) discusses the principles of genetics, their scope, the evidence on which they rest, and the bearing of these principles on the theory of evolution. Throughout the text there are figures, graphs and plates, each chapter concludes with a useful list of references and at the end of the volume is given a group of general references, a glossary, and an index.



RÖENTGENOLOGISCHE SKELETTSTUDIEN AN MENSCHLICHEN ZWILLINGEN UND MEHR- LINGEN. Ein Beitrag zu den Problemen der Konstitution und der Phylogenese. *Fortschritte auf dem Gebiete der Röntgenstrahlen, Ergänzungsband 46.*

By Franz Buschke. *Georg Thieme, Leipzig.* 25 marks (paper);  $12 \times 8\frac{1}{2}$ ; 47 + 50 plates; 1934 (paper).

X-ray studies were made on the skeletons of 25 pairs of identical twins, 18 pairs of twins of the same sex but not identical, and 7 pairs of male and female twins, and 4 sets of triplets and one set of quadruplets. Form and structure of ossification was very similar among identical twins even to the minutest details, but among ordinary twins there was found to be on the whole less similarity than between unrelated individuals of the same age and sex. However, the authors felt that the number of cases was probably too small to warrant any definite conclusions.



#### GENERAL BIOLOGY

COLLECTED SCIENTIFIC PAPERS OF SIR WILLIAM BATE HARDY, *Fellow of the Royal Society, Fellow of Gonville and Caius College, Cambridge.*

*Published under the Auspices of the Colloid Committee of the Faraday Society. The University Press, Cambridge; The Macmillan Co., New York.* \$18.00.  $10\frac{1}{2} \times 7\frac{1}{8}$ ; xi + 922 + 15 plates; 1936.

The collected scientific papers of the late Sir William Hardy enable one to trace a

steady and orderly growth of his interests. A number of excellent accounts have been published of the scientific life of Sir William Hardy, but no better epitome of his aims has been given us than that expressed by Sir Hugh Anderson, the late master of Hardy's College, Gonville and Caius: "Hardy once observed a cell divide under a microscope, and wondered why." The wonder excited in Hardy by the observation of cell division set him on the path of those investigations on physico-chemical properties of the proteins and the behavior of matter in the boundary state. Many believed that, if he had been spared, he would at long last have returned to the problem of why and how a cell divides. This is the key to the plan of his scientific life work, though it represents only one side of his many activities, a side that in the numerous appreciations that have appeared has been little touched on.

The 59 papers, most of them reprinted from the *Journal of Physiology* and the *Proceedings of the Royal Society of London* begin with a developmental study of the hydroid *Myrionotha phrygia*, continue with a series of papers on the physiology of leucocytes, and then his central problem becomes the physico-chemical properties of protoplasm. Finally there is a long series of papers on colloids and boundary phenomena. The concluding essay is a statement of the philosophical position of a biologist who sought to advance biology by a well-considered study of non-living systems. The volume is handsomely printed, fully indexed and adequately illustrated with the original lithograph and colored plates. It is altogether a fitting memorial to a remarkable man.

#### ORDER AND LIFE.

By Joseph Needham. Yale University Press, New Haven. \$2.50. 8 x 5 $\frac{1}{2}$ ; x + 175; 1936.

This volume, by the well known English biologist, is the outgrowth of three Terry lectures delivered at Yale University in 1935. The titles of the lectures are as follows: The nature of biological order; The deployment of biological order; The hierarchical continuity of biological order.

Such subjects are discussed as, the unity of natural knowledge; the cleavage between the inorganic and biological sciences, and between the theology of intelligibility and that of inexplicability; the opinions which biologists, physicists and philosophers hold regarding the form of organization which living things exhibit. The author finds that:

A careful consideration shows us that the fields of morphology and biochemistry are not so sundered as is often supposed. Organising relations are found at the molecular level and at the colloidal and paracrystalline level as well as at the anatomical level. Hardy's work, far from showing that no structure existed in the cell, showed on the contrary how subtle it must be. Although we are still in the earliest historical stages of any far-reaching organisation-calculus, we can yet see that biological order, like (but very much more complicated than) crystal order, is a natural consequence of the properties of matter, and one characteristic mode of their manifestation.

The volume is well illustrated, documented, and indexed. Altogether it is a shrewd and penetrating philosophical summary of the present status of the rapidly advancing frontiers of that broad fundamental field of biology conveniently, if not very precisely, called experimental morphology. But the parsons who administer the money for the Terry lectures must have felt a bit let down by this particular series! Such theological nutriment as may be squeezed out of the lectures is extremely dilute.

#### INVISIBLE RADIATIONS OF ORGANISMS.

By Otto Rahn. With an Introduction to the Physics of Radiation, by Sidney W. Barnes. Gebrüder Borntraeger, Berlin. 13.20 marks. 8 $\frac{1}{2}$  x 5 $\frac{3}{4}$ ; x + 215; 1936 (paper).

The author summarizes his opinions on this controverted topic as follows:

The biological part of this book has been written by a biologist who is convinced, from his own experiences as well as from the study of literature, that mitogenetic radiation exists. He has realized that it is difficult to prove it because we are dealing with an extremely weak effect, and with very sensitive detectors. Above all, we are dealing with an entirely new phenomenon, and consequently cannot predict which changes of technique might increase or decrease the effect.

It does not speak well for the present status of science that it has not been possible to settle definitely, in the course of 12 years, the question of the existence of this radiation. The fault lies equally with the two groups of contestants, those for and those against radiation.

The virtue of the book is that it presents clearly and succinctly the important literature, with complete citations, on the mitogenetic problem and its interpretation, and thus houses, in one volume, an ostensibly unbiased account of the subject. After going through the book, however, it seems probable that the reader, although feeling more informed on the many details of the subject, will still be "in the dark" about the plausibility of mitogenetic radiation itself. It is to be hoped that this book will stimulate some conclusive research.



**SALINITY AND TEMPERATURE OF THE ENGLISH CHANNEL.** *Estimation of Mean Values for the Upper Water Layer over the 25-Year Period 1903 to 1927.* Ministry of Agriculture and Fisheries, Fishery Investigations, Series II, Vol. XIV, No. 3.

By J. R. Lumby. His Majesty's Stationery Office, London. 7 shillings, postage extra.  $10\frac{1}{2} \times 7\frac{1}{2}$ ; 67 + 3 charts + 83 pp. tables; 1935 (paper).

**SALINITY AND TEMPERATURE OF THE ENGLISH CHANNEL.** *Atlas of Charts.* Ministry of Agriculture and Fisheries, Fishery Investigations, Series II, Vol. XIV, No. 3.

By J. R. Lumby. His Majesty's Stationery Office, London. 1 shilling, postage extra.  $21 \times 15$ ; 27 charts; 1935 (paper).

In order to furnish a foundation for future studies in both hydrographical and biological fields especial attention has been given in the preparation and presentation of this report "to the provision of standards embodying as much information as possible, while their representation on charts and their interpretation has been considered as of secondary importance." Fully half of the latter part of the report is taken up with tables in which data are given on (a) The positions allocated to the mean values of temperature and salinity (41 in number); (b) The general mean monthly temperature and salinity, 1903-1927; and (c) The yearly mean tempera-

ture and salinity, 1903-1927, together with the general monthly means and the general mean for the whole period. In the first half of the report occur explanatory charts, graphs and tables. There is a list of 41 references.

The group of charts issued separately exhibits the geographical relationship of the means (salinity and temperature) estimated in the above report. There are 12 charts for the months 1903-27 and a figure (same scale as charts) shows the region studied divided into rectangles and regions, and the numerical distribution of the observations.



**THE PHENOMENA OF LIFE.** *A Radio-Electric Interpretation.*

By George Crile. Edited by Amy Rowland. W. W. Norton and Co., New York. \$3.50.

$8\frac{1}{2} \times 5\frac{1}{2}$ ; 379; 1936.

The radiations emitted by this volume have the following characteristics, as stated by the author:

We shall offer evidence tending to show that the living organism is specifically adapted to the formation, storage and specific use of electric energy and that the genesis of this electric energy is due to radiant energy emitted by ultramicroscopic units or furnaces in protoplasm. These furnaces we have called *radiogenr*. We shall postulate that the combustion of the proteins is effected by these microscopic units and that the short wave radiation emitted by this continuous combustion has two primary and fundamental effects. (1) Short wave radiation knocks off electrons and thus disturbs the electrical state of the protoplasm, especially of the infinitely intricate network of the nervous system. (2) Short wave radiation so disturbs the architecture of the atom as to make the atoms chemically active, thereby forming the basis for the synthesis of protoplasm.

It seems to us unlikely that any professional biologist will regard the evidence presented as establishing the conclusions reached. In fact this book considerably increases the conviction engendered by the author's earlier excursions into the realm of theoretical biology that, as a biologist dear Dr. Crile is a great surgeon.



**PROBLEME DER THEORETISCHEN BIOLOGIE.** *Arbeiten aus dem Timirjasoff-Institut für Biologie—Moskau.*

Herausgegeben zum 15. Todestag von K. A. Timirjaseff. INRA Verlagsgenossenschaft, Moskau-Leningrad. 7 x 10; 409; 1935 (cloth). No price.

This volume is dedicated to the memory of Professor Timirjaseff, a well-known Russian plant physiologist who has also contributed much by his writings and translations to the wide-spread recognition of Darwinism in Russia of the past century. He was a foreign member of the Royal Society and delivered a Croonian Lecture in 1903. In this volume a number of papers issued from the Institute bearing his name is published in German, and thus made available to wider circles of readers. There are papers by Professor Navaschin on 'The Nature of Mutations', by Professor Tokin on regeneration, and many other contributions.



#### PROTOPLASM.

By William Seifriz. McGraw-Hill Book Co., New York. \$6.00. 9 x 6; x + 584; 1936.

A book for students in biology and medicine and the related fields of biochemistry and biophysics. The author has brought together "all those parts of the branches of science which bear upon the physical chemistry of living matter." This means that a great deal of rather technical matter, particularly mathematical, had to be included, but the author has done this with considerable skill and the volume is not too formidable for second year students. Particular attention has been given to colloid chemistry. The volume has many illustrations and is well documented and indexed.



URDEUTSCHLAND. Deutschlands Natur-schutzgebiete in Wort und Bild. Lieferungen 15, 16, 17, 18, 19.

By Walther Schoenichen. J. Neumann, Neudamm. 2 marks each. 10½ x 8½; Lief. 15, 49-72 + 9 plates; Lief. 16, 73-96 + 9 plates; Lief. 17, 97-120 + 9 plates; Lief. 18, 121-144 + 9 plates; Lief. 19, 145-168 + 9 plates.

Five numbers of this beautifully produced

and illustrated work on the natural history of Germany, earlier numbers of which have been noticed in successive numbers of this REVIEW beginning with Volume 10, Number 3.



#### HUMAN BIOLOGY

##### A HUNDRED YEARS OF ANTHROPOLOGY.

By T. K. Penniman. The Macmillan Co., New York. \$4.50. 8½ x 5½; 400; 1936. A book of great usefulness and interest. It is divided into the *Formulary period* (before 1835) "when the elements of the science are scattered throughout all the others;" the *Convergent period* (1835-59) "when efforts are made to relate the various sciences that bear on Man, ending with the admission of the high antiquity of palaeolithic man and the publication of *The Origin of Species* in 1859;" the *Constructive period* (1859-1900) which "shows a steady and confident development for the most part on evolutionary lines;" and the *Critical period* (1900-1935) when the "rediscovery of Mendel's work in 1900 introduced a more austere and critical mood," and more intensive and special research entered all branches of anthropology. The author, who is Secretary to the Committee for Anthropology in the University of Oxford, has done his work well. A general map is all that he has aimed to lay before the reader but it is clearly drawn and in the main furnishes a well balanced survey of this rapidly advancing branch of science. The general reader as well as the student will find it absorbing. There is a final section on the future of anthropology, appendixes on (1) A chronological list of men and events in the history of anthropology; and (2) Some principal congresses, anthropological museums, societies, and periodicals in various countries of the world; a lengthy bibliography and an index.



##### CRITERIA FOR THE LIFE HISTORY. With Analysis of Six Notable Documents.

By John Dollard. Published for the Institute of Human Relations by Yale Univer-

ssy Press, New Haven. \$2.50. 9 x 9; v + 288; 1935.

The author defines *life history* as "an account of how a new person is added to the [social] group and becomes an adult capable of meeting the traditional expectations of his society for a person of his sex and age." The use of life histories as a method of investigation in social psychology has been adopted only recently since some sociologists have realized, at last, that an understanding of human social relationship can only be obtained by actually studying the individual and his reactions to his particular social environment. In order to arrive at a standard method of analysis the author proposes seven criteria which he considers essential for an adequate life history. They are:

- I. The subject must be viewed as a specimen in a cultural series.
- II. The organic motors of action ascribed must be socially relevant.
- III. The peculiar rôle of the family group in transmitting the culture must be recognized.
- IV. The specific method of elaboration of organic materials into social behavior must be shown.
- V. The continuous related character of experience from childhood through adulthood must be stressed.
- VI. The "social situation" must be carefully and continuously specified as a factor.
- VII. The life-history material itself must be organized and conceptualized.

He then applies these criteria to seven well known biographic and autobiographic documents, one each from A. Adler, J. Taft, S. Freud, W. I. Thomas and F. Znaniecki, C. R. Shaw, H. G. Wells, P. Radin. The author's penetrating comments on these documents are interesting and indicate that, as he uses them, the criteria should prove helpful toward an objective study of individual social behavior. It is well to note, however, that this method is decidedly unilateral because while it describes the influence of the social group on the individual it apparently fails to take into account the fact that the individual does not remain passive but in turn exerts some influence on the group.

COSTITUZIONE E MORTALITÀ. *Pubblicazioni della Università Cattolica del Sacro Cuore. Serie Ottava: Statistica. Vol. X.*

By Alessandro Costanzo. "Vite e Pensiero," Milano. 15 lire. 10 x 6½; ix + 187; 1936 (paper).

The investigation here reported adds more evidence to that already collected regarding the diverse morbidity and mortality of individuals with different somatic constitutions. The material consists of the anthropometric data recorded for some 9000 Italian military conscripts who were born at or near Casale di Monferrato during the years 1845 to 1864, 1865 to 1880 and 1881 to 1910. The measurements of stature and chest circumference were those obtained at the medical examination to which all Italians at or around 20 years of age must be subjected in order to determine their fitness for military duty. The material is therefore unselected, and homogeneous with regard to sex, race and age. The author has investigated the ages and causes of death of these individuals. The results definitely confirm the findings of other students of the subject.

The distribution of individuals according to age at death shows that the younger dead were, on the average, those who at 20 had been of more slender build. Those dead of tuberculosis and lower respiratory infections were those who at 20 had been more slender, while those who died of circulatory and gastro-intestinal diseases were those who at the time of examination had been stocky.

The value of this study lies essentially in the fact that the material is a random sample of the population. It is to be deplored that more complete anthropometric data are not available. The biometric analysis is above reproach, but the grouping of circulatory diseases with those of the gastro-intestinal tract deserves criticism.

ABORTION—*Spontaneous and Induced, Medical and Social Aspects.*

By Frederick J. Taussig. The C. V. Mosby



Co., St. Louis. \$7.50.  $9\frac{3}{4} \times 6\frac{1}{2}$ ; 536; 1936.

The object of this monograph is: (1) to present a critical outline of the methods of diagnosis and treatment of the various forms of abortions and (2) to discuss the consequences of the legal restrictions regarding the performance of abortions. As for contraception in general and for venereal diseases, the moral and religious taboos of our civilization persist in hampering the thoughts and actions of the medical and sociological investigators of the subject. It is deplorable, as the author notes, that while apparently one out of every three or four pregnancies terminates in an abortion, the textbooks on obstetrics dedicate relatively little space to the treatment of this condition which, it is estimated, causes about 10,000 deaths of mothers yearly in the United States alone. To remedy this deficiency Professor Taussig discusses in full the anatomy and physiology of early pregnancy; the etiology, mechanism and pathology of abortion, and the symptoms, signs and methods for its diagnosis. In the following chapters he describes the several operative techniques and the advantages to be derived from each. This part is closed with a section on the complications and sequelae of abortion. There is an extensive bibliography and numerous and excellent photographs. For the human biologist the main point of interest lies in the discussion of the religious and legal taboos and how these have persisted to our day. Included is also a chapter in which the author describes his visit to a Russian abortarium.

The book closes with a plea for greater latitude in the teaching of contraceptive methods. This, the author hopes, will decrease the number of illegally produced and self-induced abortions and their harmful results. We doubt the success of such a plea, for the moralists who decry the use of both contraceptives and abortions have never been swayed by the suffering of mere mortals.



WER IST ERBGESUND UND WER IST ERBKRAK? *Praktische Ratschlge fr die Durch-*

fhrung des Gesetzes "zur Verhtung erbkranken Nachwuchses", und zur Verleihung der Ehrenpatenschaft.

*Edited under the auspices of Berliner Akademie fr rztliche Fortbildung by W. Klein. Gustav Fischer, Jena. 6.50 marks (paper); 8 marks (cloth).  $9\frac{3}{4} \times 6\frac{1}{2}$ ; xviii + 215; 1935.*

Sterilization laws naturally bring up many problems and much discussion, especially as to judgments on who should be sterilized and who allowed the pleasure of engendering future citizens. Hitler's edict of July 14, 1933 was no exception. In this book are published thirteen lectures by prominent physicians and geneticists delivered at the Berlin Academy for Medical Progress on topics pertinent to this subject as to the inheritance of various diseases and anomalies. On the whole they present a good summary of what is known, and what isn't, about the genetic transmission of disease, and most of the conclusions drawn are quite sound. However, some seem to us a little extreme, and one cannot help but wonder what would happen to the birth-rate if wholesale sterilization of persons suffering from some such discomfort as impairment of hearing should come into effect. Prefaced by extracts from the Sterilization Law and an Introduction by W. Klein, the topics and authors are as follows: Demographic-political measures in the Third Reich, by W. Klein; Foundations of genetics, by v. Verschuer; Disease of the heart and blood vessels, kidneys and blood-forming organs, by W. Weitz; Metabolic disease, diseases of the stomach, intestines and liver, and cancers, by F. Curtius; Diseases of the respiratory organs and tuberculosis, by K. Diehl; Nervous diseases, by W. Bremer; Mental diseases, by J. Lange; Diseases of the eye, by C. Adam; Diseases of the ear, by H. Claus; Children's diseases, by G. Bessau; Gynecological diseases and disturbances of the physiological functions of the woman, by G. A. Wagner; Skin diseases, by H. Gottron; Physical defects, by L. Kreuz.



ANTHROPOLOGIE STŘEDOAFRICKÝCH PYGMEJŮ V BELGICKÉM KONGU. *Anthropology*



of the Central African Pygmies in the Belgian Congo.

By Paul Schebesta and Victor Lebzelter.  
Czech Academy of Sciences and Arts, Prague.

14 $\frac{1}{2}$  x 10 $\frac{1}{2}$ ; 144 + 56 plates; 1933 (paper).

In 1929-30, the senior author conducted an expedition to the Belgian Congo for the express purpose of studying the physique of the pygmies of that region. In this report, written in both Czech and English, he presents the detailed individual measurements and somatic descriptions of the subjects, and notes regarding their social status, sex, age, and certain disease conditions. These data have been statistically summarized by the junior author. Dr. Schebesta arrives at the conclusion that most of the pygmies of this region belong to one racial group, the Bambuti; a few only show some mixture of European and Negro blood. The Bambuti are characterized by a disproportionately large head, long trunk and long, thin arms, short neck and short, thin legs, slender feet and hands. The complexion is greyish yellow, the growth of face and body hair is generally heavy. The maximum stature, observed in male adults, is less than 160 cm.; the minimum, 118 cm., is that of an adult female, mother of a fully developed six year old child. This monograph is illustrated by numerous and excellent photographs. These, together with the detailed data, will be found extremely useful by the reader, especially since the statistical treatment of the data is rather inadequate.



OUT OF THE NIGHT. *A Biologist's View of the Future.*

By H. J. Muller. *The Vanguard Press, New York.* \$1.50. 7 $\frac{1}{2}$  x 5; 127; 1935.

The author of this volume is at present serving as Senior Geneticist at the Institute of Genetics of the Academy of Sciences in Moscow. Most of the material in the book was given in a series of lectures at the University of Chicago in 1925, under the title "A Biologist's View of Progress." Section 6 (Heredity and Characters) has been since added. The central theme of the book "lies in the attempt to show that for a continuance of material,

cultural and biological progress in the human race, a thorough-going economic and social change to a more truly coöperative basis of society, together with the regeneration in human motivation attendant upon this is a prior necessity." Great stress is laid on the "possibility of positive biological improvement of mankind, *provided* the social reconstruction occurs first." In the final section are set forth the author's views on the improvement of the human race by artificial insemination. The volume is without index.



VOYAGE TO GALAPAGOS.

By William A. Robinson. Illustrated by Daniel T. West. *Harcourt, Brace and Co., New York.* \$3.00. 8 x 5 $\frac{1}{4}$ ; viii + 279 + 8 plates; 1936.

The Galapagos Islands figured prominently in the newspapers two or more years ago when the author of this volume was taken seriously ill in Tagus Cove with appendicitis. This is the story of the voyage that ended so disastrously. There were three on the little *Svaap*. From almost the beginning they found themselves in the midst of excitement—dangerous storms, a shipwreck in the jungles of Darien, and endless delays in relaunching the boat. They reached the Galapagos Islands soon after the sensational events among the little group of self-exiled Europeans, ruled by the self-appointed Empress of Galapagos, occurred. Robinson gives his version of this fantastic tale and a possible explanation of the mysterious disappearance of some of these people. The reader gets an interesting picture of the Inca coast, the Humboldt current, the Guano Islands and their bird life, and animal life in the Galapagos. The volume is illustrated but without index.



STUDIES OF THE YAQUI INDIANS OF SONORA, MEXICO. *Texas Technological College Bulletin, Vol. XII, No. 1. Scientific Series No. 2.*

By W. C. Holden, C. C. Selzer, R. A. Studhalter, C. J. Wagner and W. G.

McMillan. *Texas Technological College, Lubbock*. 60 cents postpaid. 9 x 6; 142; 1936 (paper).

During 1934 two expeditions organized at Texas Technological College proceeded to the lower reaches of the Rio Yaqui in northwestern Mexico for the purpose of studying the Yaqui Indians living there in eight historic villages. In this paper W. C. Holden, anthropologist and director of the expedition, has reported on social organization, marriage, child rearing and education, *La fiesta de gloria*, Yaqui funerals, and household economy; C. C. Seltzer, physical anthropologist of Harvard, contributed an article on "Physical characteristics of the Yaqui Indians"; C. J. Wagner, a physician, writes on "Medical practices of the Yaqui"; R. A. Studhalter, biologist, on "Yaqui agriculture," and W. G. McMillan on "Yaqui architecture." These articles with the exception of Dr. Seltzer's, were written primarily for the layman rather than the professional anthropologist.



#### LAWS OF LIFE.

By Halliday Sutherland. *Shedd and Ward, New York*. \$2.50. 7½ x 5; v + 270; 1936.

Dr. Sutherland is a well known Catholic. He tries very hard to defend his ideas on sex and population by pure logic, but his religious opinions are always evident and his biblical quotations numerous. He is opposed to contraception, sterilization and euthanasia. The "safe period" is advocated as the best biological, moral and aesthetic form of birth control. Dr. Sutherland has long been interested in population problems, and includes in this book a brief chapter on the logistic curve.

All in all "Laws of life" seems to us a slightly too ambitious title for a collection of not wholly unbiased opinions on a variety of biological and sociological problems.



#### SOUTH SEAS.

By Hugo A. Bernatzik. *Translated from the German by Vivian Ogilvie. Henry Holt*

and Co., New York. \$3.50. 9 x 6; xiv + 167 + 103 plates; 1935.

An interesting, well written popular account of various peoples and places in the Solomon Islands, New Guinea, and Bali, by a distinguished Austrian anthropologist, beautifully illustrated with over a hundred rotogravure plates from original photographs. While the author's intention in the book is popular entertainment rather than technical science, there are a good many shrewd observations and discussions relating to significant problems, such as depopulation. Making no great pretension the book as a whole is excellently done, and can be warmly recommended for the intelligent gentleman's library, the transatlantic voyager's book hamper, or even the summer vacation hammock.



#### THE MEASUREMENT OF POPULATION GROWTH. *Methods and Results.*

By Robert R. Kuczynski. *Oxford University Press, New York*. \$4.00. 8½ x 5½; vi + 255; 1936.

The author surveys a few of the methods proposed for the measure of fertility and population growth. He violently criticizes all of them except the gross and net reproduction rates which he uses and discusses at length here, as in his previous publications. His criticism is more bitter than fair since he neglects to mention that some of those indices, the use of which he censures, were not constructed for the purpose of answering the specific questions which he asks of them. The author makes much of the fact that these indices are based on census and vital statistics data, often inaccurate. The deficiencies of such data are well known to all students of population problems and the author apparently forgets that they also affect the indices which he uses. There is an appendix with useful population data for a number of countries.



#### DIE HAND UND IHRE GEHEIMNISSE.

By Adolphe Desbarrolles. *Otto Wilhelm*

*Barth, München-Planegg.* 6 marks (paper); 7.50 marks (cloth). 8½ x 5½; 313; 1935.

This translation from the works of the Frenchman, Desbarolles, who lived in Paris 1804-1866, is chiefly a plea for the reestablishment in the scientific world of the old arts of phrenology, graphology, chiromancy, and astrology. Nothing new is brought forward, the old arguments are only dressed up in new language.

Desbarolles got his start in chiromancy during a visit in Spain, when he associated with gypsies, and learned their formulae for palmistry. The book is well documented, and ought to be interesting to those for whom palm reading is a never ending source of fascination.



**DESOLATE MARCHES.** *Travels in the Orinoco Llanos of Venezuela.*

By L. M. Nesbitt. Harcourt, Brace and Co., New York. \$2.50. 8 x 5½; 320; 1936.

An interesting account of travels and adventures incidental to engineering development work in a part of Venezuela not commonly visited. The country traversed is not very exciting, and extremely trying climatically. The two chief impressions left by the book are the rankness of tropical vegetation in the atmosphere of a super-hot and super-humid green house, and the gradual but steady deterioration of the population living in such an environment.



**RASSENKUNDLICHE BESTIMMUNGS-TAFELN für Augen-, Haar- und Hautfarben und für die Iriszeichnung.**

By Br. K. Schulz and M. Hesch. J. F. Lehmann, München. 16 marks (in Germany); 12 marks (outside Germany). 3 colored and 1 black and white chart in folder 6½ x 5½ inches. No date.

This collection of hair, skin and eye color charts is in our opinion not a particularly good one. The difficulty of making such charts cannot be over-estimated, but ten shades of hair coloring seems hardly ade-

quate. The attempt to show patterns of eye pigmentation is interesting, but typical drawings might have been preferable to photographs.



**TOMORROW'S CHILDREN.** *The Goal of Eugenics.*

By Ellsworth Huntington, in conjunction with the Directors of The American Eugenics Society. John Wiley and Sons, New York. \$1.25. 8 x 5½; x + 139; 1935.

This book, written for the layman, explains the main principles of eugenics and their application to social problems. The material is clearly presented and many aspects of eugenics are considered. We feel, however, that the question and answer form could have been dispensed with. There is a classified bibliography and a good index.



**A BIBLIOGRAPHY OF SIR JAMES GEORGE FRAZER, O. M.**

Compiled by Theodore Besterman. The Macmillan Co., New York. \$4.50. 8½ x 5½; xxi + 100 + 3 plates; 1934.

Published on the eightieth anniversary of Sir James George [Golden Bough] Frazer's birth, this volume gives a complete bibliography of his work in chronological order. There is also a classified list and an alphabetical index. The work is well done, and will serve a useful purpose.



**MEN IN SUN HELMETS.**

By Vic Hurley. E. P. Dutton and Co., New York. \$2.50. 8½ x 5½; 252; 1936.

A realistic and interesting account of life in the Philippines. The author shows the danger, discomfort and monotony of the tropics as well as the romance.



**BULLETIN DER SCHWEIZERISCHEN GESELLSCHAFT FÜR ANTHROPOLOGIE UND ETHNOLOGIE 1935/36. 12 Jahrgang.** [*Bulletin de*

la Société suisse d'Anthropologie et d'Ethnologie 1935/36. 12<sup>me</sup> année].

Sûge de la Société, Institut anthropologique de l'Université, Plattenstr. 9, Zurich 7.  
9 x 6½; 20; 1936.



## ZOOLOGY

OCEANIC BIRDS OF SOUTH AMERICA. *A Study of Species of the Related Coasts and Seas, Including the American Quadrant of Antarctica Based Upon the Brewster-Sanford Collection in the American Museum of Natural History. Vols. I and II.*

By Robert C. Murphy. Illustrated from Paintings by Francis L. Jaques. American Museum of Natural History, New York.  
\$10.50 per set. 10½ x 7½; xxiii + 1245 + 72 plates; 1936.

During the years 1912-1917 the Sanford-Brewster expedition under the direction of Mr. Rollo H. Beck made the first organized trip of its kind around South America to undertake a systematic field study of sea birds. In these volumes Dr. Murphy has ably organized and presented the great wealth of data accumulated as a result of this expedition. He has also incorporated material from various other sources which would aid in giving a greater completeness to the study.

Part I (first half of Volume I), prefaced with a brief narrative of the Brewster-Sanford expedition, is given to the consideration of the physical environment of the regions—geographic background and hydrology in relation to oceanic birds. Part II (last half of Volume I and all of Volume II) is devoted to the life histories of some 183 species and subspecies of oceanic birds. The selection of species and forms for consideration in these biographies was based upon geographical criteria rather than blood relationship. The forms chosen fall ecologically into the four groups of littoral, inshore, off-shore and pelagic birds. Two forms are described as new in this book. The nomenclature of Peter's *Check-List* has been used.

Eighty text figures, 16 colored plates, 72 photographs, a bibliography and index complete these carefully prepared and valuable volumes.

LAND OF ELEPHANTS. *Big-Game Hunting in Kenya, Tanganyika and Uganda.*

By Count Zsigmond Széchenyi. Putnam and Co., London. 12s. 6d. net. 8½ x 5½; xi + 209 + 96 plates; 1935.

AFRICAN ADVENTURE. *Letters from Famous Big-Game Hunters.*

Edited and Annotated by Denis D. Lyell. E. P. Dutton and Co., New York. \$3.75.

8½ x 5½; xv + 270 + 8 plates; 1935.

Both these books deal with hunting adventures and exploits in Africa; Count Széchenyi's in Kenya, Tanganyika, and Uganda in the immediate past; Mr. Lyell's over a wider field and time. Both will be enjoyed by all sportsmen, naturalists, and students of animal behavior.

Count Széchenyi is a young and handsome Hungarian nobleman devoted to big-game hunting and life in the wild. His book is made up of extracts from his field diaries; episodic rather than continuing narrative. Its most noteworthy feature is the large number of photographs reproduced as half-tone plates. The author was nearly or quite as much interested in photography as in shooting. Some of the lion pictures are quite extraordinary. Of particular interest to biologists is the picture of a herd of zebra, showing the camouflaging effect of the pattern as distance increases. There is a long and interesting chapter on termites, based upon the work of Escherich and to some slight extent on the author's own observations.

Mr. Lyell's book is made up of letters that he has received from famous big-game hunters, mostly British, interlarded with his own comments upon points suggested by the letters. These comments and annotations are always shrewd, and on the whole more interesting than the letters, many of which it must be confessed are a bit dull and trivial. Mr. Lyell is a Scot of vast experience in African big-game hunting, and a practical kind of person. Anyone making a first hunting trip to Africa will make a mistake if he does not take this book along and ponder over the wisdom it contains.

PROCEDURE IN TAXONOMY. *Including a reprint of the International Rules of Zoological*

*Nomenclature with Summaries of Opinions  
Rendered to the Present Date.*

By Edward T. Schenk and John H. McMas-  
ters. Stanford University Press, Stanford  
University, Calif. \$2.00. 9 x 6; viii +  
72; 1936.

"This book was prepared for the purpose of supplying the student as well as the professional systematist with (1) a clear-cut and comprehensive statement of the principles of taxonomy; (2) the International Rules of Zoölogical Nomenclature; (3) Summaries of Opinions rendered to the present date; (4) a complete index—the only index of the rules and summaries ever published." Many readers will be surprised by the technicalities and legal aspects offered by the field of taxonomy. Much of the book reads like a textbook on torts. One list, which the reviewer found both interesting and alarming, consisted of a series of terms used in describing zoölogical groups of various degrees and kinds. At the risk of some tedium this list is appended: "Aberration, blastovariation, branch, class, cohort, conspecies, division, family, form, gens, genus, jordanon, kingdom, legion, morpha, mutation, nation, order, phalanx, phratry, phylum, proles, race, section, series, species, subclass, subfamily, subgens, subgenus, subkingdom, suborder, subphylum, subspecies, subtribe, subvariety, superclass, superfamily, superform, supergenus, superorder, supertribe, supervariant, supervariety, tribe, variant, variety." This, as the authors say, is only a "partial" list!



OUR ENEMY THE TERMITH.

By Thomas B. Snyder. Comstock Publish-  
ing Co., Ithaca, N. Y. \$3.00. 9 x 6;  
xii + 196; 1935.

Dr. Snyder is probably better fitted to write a book of this type than any other man working in the field today as his experience has taken him into all the phases of termitology since his early association with Dr. Nathan Banks more than twenty-five years ago. The book discusses termites from the earliest known fossil forms to those of the present day; their biology, behavior, structure, and

extermination. Fortunately the author has been in close touch with all these phases, both in the United States and in several tropical countries. The reader is introduced into the field of termite control by such methods as wood preservation, building codes, poisons, and biological control. One easily grasps the notion that the termite problem actually is on the increase in many locations due to conditions created by man which are especially favorable to termite increase. Dr. Snyder's dissertation on anthropocen-  
tricism should be read by everyone who endows the social insects with super-  
natural powers. The book will serve as a good antidote for the works of Maeterlinck and other romantic biologists.



MAMMALS OF INDIANA.

By Marcus W. Lyon, Jr. American Mid-  
land Naturalist, University of Notre Dame,  
Notre Dame, Indiana. \$3.00. 9 x 5½;  
384; 1936.

The material appearing in this book is reprinted from the "American Midland Naturalist" and is an attempt, "... to bring up to date the main facts of the mammalian fauna of Indiana and make them available in a single volume without recourse to the published writings of others more or less hidden away in serial publications containing other matters."

The mammals are taken up systematically starting with the opossum and ending with Jefferson's ground-sloth. For each species discussed, data are given about the taxonomic synonymy; the general geographic range including the local Indiana records; the description of the form; the ecologic habitat; the breeding activities, and other miscellaneous items. There are several taxonomic keys which should prove useful and a number of maps reporting the distribution of the species in question throughout the various counties of the state. An extensive bibliography is also appended.

The book has been prepared in a workmanlike manner and should prove of considerable service to mammalogists of Indiana and adjoining states.

THE MIGRATION OF NORTH AMERICAN BIRDS. *United States Department of Agriculture Circular No. 363.*

By Frederick C. Lincoln. U. S. Government Printing Office, Washington. 10 cents. 9½ x 5½; 72; 1935 (paper).

The extensive program of bird-banding carried on by the Biological Survey for many years has resulted in important records bearing on bird migration, and this pamphlet is a very successful presentation of the major results for the benefit of biologists and bird lovers. Numerous maps show the areas in which certain species of birds spend the breeding season, areas in which they winter, and routes they follow in migration, while isochronal lines show approximately the time consumed in migration. The theories advanced to account for bird migration are summarized briefly, additional facts are presented and a few generalizations are expressed. A bibliography and an excellent index, listing both English and Latin bird names, help to make this a most useful publication for everyone interested in birds.



HUNTING WILD LIFE WITH CAMERA AND FLASHLIGHT. *A Record of Sixty-five Years' Visits to the Woods and Waters of North America. Vol. I. Lake Superior Region. Vol. II. Wild Life of Coasts, Islands, and Mountains.*

By George Shiras, 3d. National Geographic Society, Washington. \$5.00 the set. 10 x 6½; Vol. I, xxi + 450; Vol. II, viii + 450; 1935.

George Shiras, 3rd, author of these two beautiful volumes of portrait and word pictures of wild life in North America, was the originator of flashlight photography of wild animals, a technique that he has developed into a fine art. The reproductions here of 950 of his fine photographs can leave no one in doubt as to the high degree of perfection this art has reached during his many years of persistent endeavor to make hunting with the camera a sport not to be excelled by that of hunting with a gun. The book is published by the National Geographic Society, in whose magazine much of the

text and many of the photographs of these volumes have appeared over a period of years. Volume I is concerned with the wild life of the Lake Superior region, and Volume II with the wild life of coasts, islands and mountains. There is an index to Volume II, but none to Volume I.



EIN LEBEN FÜR TIERRH.

By Johannes Gebbing. *Bibliographisches Institut AG., Leipzig.* 5.80 marks (25 per cent reduction outside Germany). 9 x 6½; 290 + 65 plates; 1936.

In addition to Gebbing's autobiography and a history of the development of the Leipzig Zoo during the past 25 years under the author's directorship, this book contains much interesting material on the life and behavior of animals in their native habitats, in the zoo, and in the films and circus. The author writes from first-hand knowledge. He himself took part in the expeditions to collect what is reputed to be the largest collection of lions in any zoo, and also other animals, and was not averse to hiring out both some of the animals and himself to cinema companies and circus arenas during the war and inflation years to raise money for the up-keep of his collection. An interesting book, nicely illustrated, mostly with animal portraits.



THE MIGRATIONS OF ANIMALS FROM SEA TO LAND.

By A. S. Pearse. *Duke University Press, Durham, N. C.* \$3.00. 8½ x 5½; x + 176; 1936.

In this book an attempt is made to condense the available facts bearing on the migrations of animals from sea to land. One chapter is devoted to the principal routes of migration, one to the causes of these migrations, and one to changes which animals have undergone in their movement from sea to land. The method of presentation is somewhat novel and in several cases (e.g., the salmon and soft shelled clam) not entirely consistent with facts. It seems regrettable that more

time could not have been given to a wider appreciation of certain important topics so that the review included in the text might give a clearer and more accurate picture to the student. The bibliography includes over 700 references and represents one of the best features of the book. The volume is recommended to students interested in physiological ecology and marine biology.



PRÉCIS DE BIOLOGIE ANIMALE. *A l'Usage des Candidats au Certificat d'Études Physiques, Chimiques et Biologiques et à la Licence des Sciences.*

By M. Aron and P. Grassé. Masson et Cie, Paris. 80 francs. 7½ x 5½; viii + 1009; 1935.

This is a French zoological text prepared, "A l'usage des candidats au certificat d'études physiques, chimiques et biologiques et à la licence ès sciences." It differs not fundamentally in organization from the many similar books in English which devote about half of their space to a discussion of biological principles—structure and function of protoplasm, cytology and heredity, general physiology, ecology, etc.—and the remaining half to a systematic review of the animal phyla. The book has the virtues of clear organization, numerous drawings, and an extensive index and table of contents. It is typographically superior to the usual run of French textbooks.



A GUIDE TO HUMAN PARASITOLOGY for Medical Practitioners. *Second Edition.*

By D. B. Blacklock and T. Southwell. William Wood and Co., Baltimore. \$4.00. 9½ x 6; viii + 259 + 2 plates; 1935.

This book on practical parasitology for the clinician (previously reviewed in Q. R. B., Vol. 8, p. 232) has been revised slightly in its second edition by the omission of certain material which the authors felt "incapable of adequate treatment in an elementary textbook of this nature." Comparison of the table of contents of the two editions shows that the omitted material, totalling eleven pages, concerned

itself with the drugs used in the treatment of certain of the diseases discussed in the text.



INTRODUCTION TO HUMAN PARASITOLOGY. *Fifth Edition, Rewritten and Enlarged.*

By Asa C. Chandler. John Wiley and Sons, New York. \$5.00. 9 x 5½; xvi + 661; 1936.

This successful and important textbook has been revised in its fifth edition by the inclusion of new material in the chapters dealing with the spirochaetes, amoebae, malaria, rickettsias, flukes, Strongyloides, filariae and myiasis; by alteration of the arrangement and organization of certain of the chapters with the view of making them easier for students to follow, and, by making a few changes in nomenclature and classification. Brought up to date as it is, it should continue to serve students of general human parasitology. There is a short bibliography and an index.



UNTERSUCHUNGEN ÜBER DIE TIERWELT DES WIESENBOSENS.

By Gerhard Frenzel. Gustav Fischer, Jena. 6 marks. 9½ x 6½; v + 130; 1936 (paper).

The data concerning the metazoa found in the meadow-lands of Germany described in this book include: distribution, population density in different localities and at different seasons, life histories, type of soil, soil temperature, depth at which the metazoa were found, etc. Several varieties of Nematoda not previously described for Germany are included. Bibliography and author and subject indices are provided.



AN AVIARY ON THE PLAINS.

By Henry G. Lamond. Angus and Robertson, Sydney. 6 shillings. 7½ x 4½; viii + 228; 1934.

This book records the observations of a non-scientific bird lover on the birds inhabiting a hypothetical aviary in Australia lying between the 137th and 139th degrees of longitude and the 20th and 22nd

degrees latitude. The interspersing of numerous contractions and colloquialisms such as 'em for "them," "the old girl" in designating a female bird, etc., will be irritating to those who enjoy a different type of English, and will insofar detract from the pleasure one might derive from these otherwise rather pleasing descriptions of bird life. The book has no index.



#### A NATURAL HISTORY OF THE SEAS.

By E. G. Boulenger. D. Appleton-Century Co., New York. \$3.00. 8½ x 5½; 215 + 9 plates; 1936.

The author, Director of the London Zoological Society's Aquarium, has written a book for the general reader. He has made a survey of the teeming populace of the ocean, pointing out the various groups, and describing with considerable detail some of the more interesting members of the groups. The numerous sketches and photographs will help the reader to recognize these forms readily wherever he may come upon them. The volume is indexed.



#### REPORT ON THE MALDON (ESSEX) PERIWINKLE FISHERY. Ministry of Agriculture and Fisheries. Fishery Investigations, Series II, Vol. XIV, No. 6.

By F. S. Wright. His Majesty's Stationery Office, London. 2 shillings. 10½ x 7½; 37; 1936 (paper).

This report embodies a valuable review of information on the natural history of the intertidal gastropod *Littorina littorea* and allied species as well as certain original contributions to our knowledge of the abundance, rate of growth, and the practical aspects of the fishery of *Littorina littorea* in the region of Maldon (Essex), England.



DIE TIERISCHEN PARASITEN der Haus- und Nutztiere, sowie des Menschen. Ein Lehr- und Handbuch mit Bestimmungstabellen für Tierärzte, Ärzte und Studierende. Dritte, umgearbeitete Auflage.

By Josef Fiebiger. Urban und Schwarzenberg, Berlin. 17.50 marks (paper); 19 marks (cloth). 10 x 7; xii + 375; 1936. The third edition of a well known and widely used text on animal parasitology. The book is divided into two sections. Part I deals with general descriptions of parasites, their life cycles, hosts, etc. Part II is a detailed classification and description of the different groups of parasites. The book is well illustrated.



#### REPORT ON INVESTIGATIONS INTO THE CONDITIONS OF CERTAIN OF THE OYSTER BEDS IN THE SOUTH WALES SEA FISHERIES DISTRICT (June, 1934). Fishery Investigations, Series II, Vol. XIV, No. 5.

By F. S. Wright. His Majesty's Stationery Office, London. 2 shillings net. 10½ x 7½; 29 + 3 charts and 1 map; 1935 (paper).

Investigations undertaken to improve the South Wales oyster fishery are described. Results of the experimental relaying of Portuguese oysters in local areas are discussed and, in addition, the author has included recommendations with respect to future experimental work designed to increase the stock of local oyster beds.



#### TURTLE SHIELDS. Pocket Natural History, Zoological Series No. 1.

By Harold L. Madison. Cleveland Museum of Natural History, Cleveland, O. 7½ x 5½; 4; 1934 (paper).

An extremely useful little leaflet that makes easy the identification of some 16 species of common turtles from external (carapace) characters. Every teaching zoologist should have this at hand.



#### A CHILD'S STORY OF THE ANIMAL WORLD.

By Edward G. Huey. Illustrated by H. R. Daugherty and Olive Earle. Reynal and Hitchcock, New York. \$3.50. 9 x 7; 355 + 30 plates; 1936.

This is a charming zoology book for children. It is clearly and interestingly



written and the subject matter is in logical sequence. The photographs and drawings are excellent and there is a good index.



FLORIDA FISHES. *Pocket Natural History No. 5. Zoological Series No. 2.*

By Harold L. Madison. Cleveland Museum of Natural History, Cleveland, Ohio. 25 cents.  $6\frac{1}{2} \times 3\frac{1}{4}$ ; 32; 1936 (paper) [In envelope].

This booklet lists a number of Florida fishes and gives a brief description of the appearance and habits of each. It is well illustrated and there is an index.



### BOTANY

HUMUS. *Origin, Chemical Composition, & Importance in Nature.*

By Selman A. Waksman. Williams & Wilkins Co., Baltimore. \$6.50.  $9 \times 5\frac{1}{2}$ ; xi + 494; 1936.

As an addition to the author's *Principles of Soil Microbiology* this new book on humus represents a noteworthy contribution to the field for which a need has long been felt. It is based on extensive work of the author and his coworkers as well as a thorough review of the literature. The volume contains 17 chapters which are considered in three parts, namely: a historical account of the chemical nature of humus, its formation and rôle in plant nutrition; origin in nature of humus; and the decomposition of humus, its functions and applications. The book includes also an account of methods of humus analysis. An extensive bibliography, consisting of 1311 references, adds greatly to the value of the book.

The problem of humus is not only of scientific interest but is also fundamental to aquiculture and agriculture. The large scope covered by the treatise makes it helpful to those interested in different aspects of soil study as well as to those working on problems connected with research in salt and fresh waters.

### PRACTICAL PROBLEMS IN BOTANY.

By Wilfred W. Robbins and Jerome Isenbarger. John Wiley and Sons, New York.

\$2.00 net.  $8 \times 5\frac{1}{4}$ ; ix + 402; 1936.

Unfortunately many of these problems do not seem to us very practical so far as high-school students are concerned. Some of the problems that immature minds are asked to pass upon, are still unsolved after decades of research, and in the case of too many other questions there are no clues elsewhere in the book for a boy or girl to follow up. However, much that is good may also be said for this work. Broad principles are emphasized throughout and the authors are successful in their aim "to lay a foundation of fundamental principles which will enable pupils to develop an understanding of the significance of plant life which is such an important part of their environment." To bring out the best results from its use as a high-school text, however, the book should undeniably be in the hands of an unusually good teacher. The annotated bibliographies should be useful in selecting books for a school library. There is an index.



ELEMENTARY BACTERIOLOGY. *Third Edition, Revised.*

By Joseph E. Greaves and Ethelyn O. Greaves. W. B. Saunders Co., Philadelphia. \$3.50 net.  $7\frac{1}{2} \times 5\frac{1}{4}$ ; 562; 1936.

The third edition of this excellent elementary textbook contains numerous additions to the subject matter treated in the previous editions (reviewed in Q. R. B., Vol. 4, p. 141; Vol. 7, p. 365). Yeasts, molds and actinomyces are discussed much more extensively and in a separate chapter. Other additions include a chapter on temporary and hereditary variations of bacteria, one on their chemical activities, and another on the lethal effect of certain chemicals on the bacteria. The popularity of this book is well deserved.



БИОХЕМИЯ КУЛЬТУРНЫХ РАСТЕНИЙ. Том I. Хлебные злаки. Н. Н. Иванов, Главный,

редактор. Государственное издательство сельскохозяйственной литературы, Москва-Ленинград. Брун. 80 коп.; 320; 1936.

[BIOCHEMISTRY OF CULTIVATED PLANTS. Vol. I. Cereals.

Edited by N. N. Ivanoff. State Publishing House for Agricultural Literature, Moscow-Leningrad. 5.80 roubles. 7 x 10; 320; 1936 (cloth)].

The book gives a description of the chemical composition of cereals and a great attention is paid to the qualitative characteristics of the main compound substances in the plant, their accumulation and conversion in the plant organism during the vegetative period and storage in the seed. This first volume treats wheat, oats, corn, rice, millet and buckwheat. There are included an English foreword and table of contents.



SILVA FENNICA 34. *Viljavan Maa-alan Jakautumisesta Sekä Lehtokasvillisuudesta ja -Kasvistosta Keskisen Längelmäveden Seudulla*. [Über die Verteilung des fruchtbaren Bodens sowie über die Hainvegetation und -Flora in den Gegenden um die Mitte des Sees Längelmävesi].

By Olavi Cajander. Society of Forestry in Suomi, Helsinki. 9½ x 6½; 37; 1934 (paper). SILVA FENNICA 35. *Yksityismetsien Työtarjonnasta*. [Über das Arbeitsangebot in den Privatwäldern].

By P. J. Pelittari. Society of Forestry in Suomi, Helsinki. 9½ x 6½; 17; 1935 (paper).

SILVA FENNICA 36. *Metsänhoitolaitoksen 75-Vuotisjuhla 19 19/IV 34*. [75 Years' Jubilee of the Finnish Forest Service on April 19th, 1934].

Society of Forestry in Suomi, Helsinki. 9½ x 6½; 78 + 1 plate; 1935 (paper).

ACTA FORESTALIA FENNICA 41. *Publications of the Society of Forestry in Suomi*. Containing following articles: *Puiden vikaanisuudesta Pohjois-Suomen metsissä*. Tilastollis-metsätaloudellinen tutkimus. [Referat: Über die Schädlichkeiten der Bäume in den Wäldern Nord-Suomis (-Finlands). Eine statistisch-forstpathologische Untersuchung] by P. S. Tikka; *Koivun juuristo* [Summary: The root system of birch, *Betula verrucosa* and odorato], by Erkki Laitakari; *Kuusen juuri-*

*ston ensi kehityksestä* [Referat: Die erste Entwicklung des Wurzelwerks der Fichte] by Martti Hertz; *Tutkimuksia metsikön ja kasvupaikan vaikutuksesta kuusen rungon kehitykseen* [Referat: Untersuchungen über die Einwirkung des Bestandes und Standortes auf die Qualität des Fichtenstammes] by Erkki Laitakari.

Helsinki. 9½ x 6½; 702 + 44 plates, 1935 (paper).



## MORPHOLOGY

THE CRANIAL MUSCLES OF VERTEBRATES.

By F. H. Edgeworth. University Press, Cambridge; The Macmillan Co., New York.

\$30.00. 12½ x 9½; x + 493; 1935.

This is a superbly reproduced volume, handsomely bound, attractively printed and replete with excellent pen and ink drawings. It does credit to the printers' art. The book also does credit to its subject-matter and author since it summarizes, with admirable clarity and organization, much of the knowledge existing on the cranial musculature of vertebrates. The emphasis of the book is modestly stated by the author in the preface in which he says,

Many investigations have been carried out during the last century and a half on the comparative anatomy and embryology of the cranial muscles of Vertebrates and of their motor nerves. I have attempted in this volume to give a summary of the knowledge that has resulted and used it to determine as far as possible the primitive cranial musculature and lower motor neurons in each of the Vertebrate phyla. The ultimate object was to ascertain what evidence this gives on the problems of their genetic relationships and so of the phylogenetic history of Man in the remote past.

For specialists in this field and for comparative anatomists generally this volume will be heartily welcomed as a detailed summary of much morphological data. The most unfortunate thing about the book is that, by virtue of its size and elaborate format, its price will be prohibitive for many students.



EINFÜHRUNG IN DIE VERGLEICHENDE BIOLOGISCHE ANATOMIE DER WIRBELTIERE.

*By Hans Böker. Gustav Fischer, Jena.*  
12. marks (paper); 13.50 marks (cloth).  
10½ x 6½; xi + 228; 1935.

In this first volume of an introduction into comparative anatomy of the vertebrates the author has departed from the classical method of presenting comparative anatomy, the method in which emphasis is laid upon homology, and instead makes an attempt to unite the anatomical features with the life habits and environmental circumstances of the animal. In order to illustrate the dependence of form upon function, the book is divided into two main sections, the first of which deals with morphology of basic types of forms from unicellular animals down to primitive mammals; the second and by far the largest part of the book is concerned with the biological anatomy of locomotion. Seven different types of locomotion are discussed at great length in their relation to each of the classes of vertebrates. They are respectively, climbing, flying, walking and running, jumping, the upright locomotion characteristic of man, underground movements such as digging and burrowing, and swimming and diving. The author points out again and again in the book that methods of locomotion determine the habits and appearance of an animal. The second volume will deal with the anatomy of nutrition and reproduction. An important book.



#### TRAITÉ D'EMBRYOLOGIE DES VERTÉBRÉS.

*By A. Brachet. Second edition revised and completed by A. Dalcq and P. Gérard. Masson et Cie, Paris.* 110 francs (paper); 130 francs (cloth). 9½ x 6½; viii + 690; 1935.

This is a new edition of an important embryological volume originally written by the distinguished Belgian biologist, Albert Brachet. The book has been revised by rewriting and modernizing certain parts of the text; especially the chapters dealing with gastrulation and formation of the embryo, foetal annexation and origin of the germ cells, and, by the addition of a number of new and very effective illustrations. The book is of reference calibre in that it deals minutely

with many of the problems of vertebrate embryology. The text is divided into two major divisions; the first called "General Embryology" comprising a discussion of such problems as reproduction in general, structure and formation of the sex cells, fecundation, cleavage and blastulae formation and gastrulation and embryo development as illustrated by the various vertebrate groups. The second division, called "Special Embryology," is devoted to the numerous topics of organogeny. Each chapter is followed by a well-chosen and extensive bibliography.

This book, in its new edition, remains a significant and important contribution to the study of ontogeny.



#### PHYSIOLOGY AND PATHOLOGY

##### THE SPECIFICITY OF SEROLOGICAL REACTIONS.

*By Karl Landsteiner. Charles C Thomas, Springfield, Ill.* \$4.00 postpaid. 9 x 5½; viii + 178; 1936.

The chemical aspects of immunological reactions are those in the main emphasized in this comprehensive review by a master in the field. The subject is of great importance from the point of view of general biology, especially on the theoretical side, because through immunological reactions it has been demonstrated that in living organisms chemical differences parallel differences in morphology, and with corresponding degrees of specificity. The complexity of the situation is comparable to the complexity of life itself.

The various proteins in one animal species, distinguishable by their composition and physicochemical properties, are also quite different serologically and in consequence the serum reactions reveal a two-fold specificity, that of the particular protein and, for each, that of the species. Blood serum contains at least four serologically distinct species specific proteins (globulin, fibrinogen, serum mucoid, albumin) and likewise in milk and eggs several protein antigens are demonstrable. When sera are produced with such mixtures the various antibodies corresponding to the single components can be separated without difficulty by partial precipitation. In such an experiment, after addition of a sufficient amount of horse globulin to an anti-horse, immune serum possessing precipitins for both globulin and albumin, the supernatant fluid obtained by centrifuging no longer acted on globulin, though still with undiminished intensity on albumin.

The book is extensively documented bibliographically and indexed as to subjects. It is a valuable addition to the literature of general biology as well as medicine.



#### DISEASE AND DESTINY.

By Ralph H. Major. D. Appleton-Century Co., New York. \$3.50. 8 x 5½; xiv + 338 + 37 plates; 1936.

A book for the general reader. The author, Professor of Pathology in the University of Kansas Medical School, writes of the diseases that have had a profound effect upon world history. He shows how the destinies and thoughts of the masses have been deeply influenced by the diseases that have afflicted rulers, writers, artists and men of power. Typhus fever ended the life of Franz Schubert as well as of many lesser lights. Dürer died of malaria and St. Francis of Assisi and Molière of tuberculosis. Francis, in his youth, a gay leader of the revelers of Assisi, went through a spiritual crisis when ill of tuberculosis and subsequently became the founder of the great Order of St. Francis. It was Molière's experiences with the doctors, while ill, which supplied him with much material for his great comedies. The life of Henry the Eighth, and English history were profoundly effected by Henry's first wife (probably a syphilitic) bearing him four still-born sons and one daughter (Bloody Queen Mary). Nietzsche was probably a paretic during most of the time that he was producing his writings which so deeply influenced European and American thought. Leprosy is reviewed from early times to the present. Father Damien and his work among the lepers and his subsequent death from this dread disease are given much space. Hemophilia, the curse of some of the ruling families of Europe, is discussed in the final chapter—particularly in relation to the last royal family of Russia and the devastating influence of Rasputin, whose power as a healer was sought after other sources had been exhausted in the search of a cure for the young heir to the throne.

The volume contains numerous illustra-

tions, many of them reproductions of famous portraits and etchings, or frontispieces of books, and is indexed. Doctor Logan Clendening contributes a preface.



THE INTEGRATION OF THE ENDOCRINE SYSTEM. *Being the Fifth Horsley Memorial Lecture, Delivered at University College Hospital Medical School.*

By Sir Walter Langdon-Brown. The University Press, Cambridge; The Macmillan Co., New York. 75 cents. 7½ x 4½; 54; 1935 (paper).

The purpose of this lecture was to show that both nervous and hormonal effects are important in the integration of the endocrine system. The author bases his remarks on the following three lines of advance:

1. The diencephalon (particularly the hypothalamus) has been conclusively shown to be the nervous structure concerned with the expression of the emotions.
2. The pituitary, which is so closely associated with the diencephalon, has become the leader of the endocrine orchestra.
3. It is now realized that all nervous impulses have a chemical mediator between the neuron and the tissue cell, and indeed between one neuron and another.

Growing out of this background the author visualizes the ductless glands performing their duties steadily and properly according to the biochemical demands placed on them by the body, but also, subject to much modification of their activity at certain times due to the nervous intervention of the diencephalon.

This is an interesting and scholarly lecture which synthesizes much basic material about the operation of the endocrine system as an integral, almost teleological, part of the organism.



#### A BASIS FOR THE THEORY OF MEDICINE.

By A. D. Speransky. Translated and Edited by C. P. Dutt with the Collaboration of A. A. Subkov. International Publishers, New York. \$4.00. 9 x 6; 452; no date.

This is a remarkable book, impossible to review adequately in a brief paragraph because it is made up of a mass of experi-

mental details and theoretical interpretations of them, without any clear cut general organization of the material into a unified whole. It represents well the best and the worst of Soviet science today; extraordinary brilliance and originality of experimentation and detailed thinking, on the one hand; painfully little and inadequate coherent organization of ideas, synthesis, and generalization.

One aspect of Speransky's position can be put in this way. The current view of the mechanism of infectious disease is that the disease arises from the victory of an invading microbe over the defensive resources of the organism—a view which holds also that the whole course of the disease is determined by the struggle between the micro-organism and its host. Speransky, on the contrary, argues that not only the course but the cause of the disease changes with every stage. It is a process depending on the interaction of many parts. It should be pictured as a chain of reactions, proceeding essentially in the nervous system, with every link determined by its predecessor.

We strongly recommend the reading of this book to medical men, physiologists, and general biologists.



#### LA RENAISSANCE DE LA MÉDECINE HUMORALE.

By *Auguste Lumière*. *Léon Sézanne, Lyon*.

20 francs. 8½ x 5½; xi + 204; 1935.

This is a diffuse and rather vague exposition of the author's theory regarding the humoral changes associated with disease. It is contended that, since a number of substances which enter into the composition of body cells and tissues are in the colloidal state and since metabolic changes and toxins will cause flocculation of the colloids, the precipitates will irritate the sympathetic nerve endings and give rise to such conditions as asthma, anaphylactic shock, etc., and the symptoms which accompany fevers, vomiting, headaches and the like. Therefore, he concludes, whenever humoral changes accompany disease, the patient should be treated with

substances that either will assure greater stability of the colloids or will decrease the irritative power of the precipitates. He has found that magnesium hyposulphate among other things has these properties, and in the reports of successfully treated asthma cases the efficacy of this compound as a therapeutic agent is extolled.

Much to the author's manifest chagrin this theory, which he has advanced since 1921, has attracted little or no attention in medical circles. The reasons for such disregard are not very difficult to understand. The introduction to this volume contains an excellent summary of the history of humoral theories in medicine.



LE TESTICULE. *Organe Elaboreur de l'Hormone Sexuelle Mâle. Actualités Scientifiques et Industrielles* 259. *Exposés de Biologie. La Cellule Germinale dans l'Ontogenèse et l'Évolution*, III.

By *Jacques Benoit*. *Hermann et Cie, Paris*. 15 francs. 10 x 6½; 64; 1935 (paper).

L'OVAIRE. *Organe Elaboreur des Hormones Sexuelles Femelles. Les Hormones Sexuelles chez les Intersexués. Actualités Scientifiques et Industrielles*, 260. *Exposés de Biologie. La Cellule Germinale dans l'Ontogenèse et l'Évolution*, IV.

By *Jacques Benoit*. *Hermann et Cie, Paris*. 15 francs. 10 x 6½; 68; 1935 (paper).

These two brochures contain a very good review of the literature, together with a presentation of some work of the author, on the development of the ovary and testes. There is nothing essentially new. From morphological and histophysiological studies on birds, fishes, amphibians, reptiles and mammals the author confirms the notion held by some other workers in the field that the embryonic gonad, male or female, is originally bi-sexual, and that whether it develops into ovary or testis is determined by the cortex-medulla complex. It is suggested that even among normals an activity of a hetero-sexual hormone can be realized up to a certain point and only slightly impair a one hundred per cent sexuality.

A BIBLIOGRAPHY OF TWO OXFORD PHYSIOLOGISTS, RICHARD LOWER 1631-1691, JOHN MAYOW, 1643-1679. *Oxford Bibliographic Society Proceedings and Papers, Vol. IV, Part I. i, 1934.*

By John F. Fulton. *Oxford University Press, Oxford.* 10 shillings. 10 $\frac{1}{2}$  x 7 $\frac{1}{2}$ ; 62 + 6 plates; 1935 (paper).

This bibliography is of value because it represents the works of two scientists who were among the first to enter the field of experimental physiology at Oxford University. The author, who has already prepared a bibliography of Robert Boyle and hopes in the future to compile other bibliographies of men prominent in Oxford science during the Restoration, gives all the known editions of these men's writings together with notes, explanations and discussions. Dr. K. J. Franklin contributes an introduction to Lower. Naturally, it is Lower's bibliography that is now of greater importance and interest, but during their time, both Lower and Mayow were widely read, as this list of their works with frequent editions testifies. The author includes brief biographies of both, and sections regarding those writings in which their work was discussed and criticized. Reproductions of a number of facsimiles of title pages add considerable interest to the text. Technically the work maintains the high standards of the author's earlier excursions into the field of bibliography.



L'IVRESSE (*Physiologie de l'aliment excitant*). *Actualités Scientifiques et Industrielles*, 265.

By J. A. de Loureiro. *Hermann et Cie, Paris.* 10 francs. 10 x 6 $\frac{1}{2}$ ; 38; 1935 (paper).

Physicians and physiologists, whether they believe that alcohol and other stimulants are harmful to man or whether they believe them beneficial, apparently overlook the most important point, which is that man has recourse to stimulants because he desires them. This is the substance of the author's brief but interesting discussion on inebriety. While it is principally of alcoholic inebriety of which he speaks, the term used is intended to

cover the state of excitation due to sexual, religious, artistic and other stimuli. In his opinion, the desire for these as well as for alcoholic stimulants are typically human and should be considered as such by the physiologist.



THE AVIAN VISUAL SYSTEM. I. *Cerebral Function of the Domestic Fowl in Pattern Vision. Comparative Psychology Monographs, Vol. 12, No. 3, Serial No. 58.*

By John D. Layman. *Johns Hopkins Press, Baltimore.* 75 cents. 10 x 7; 36; 1936 (paper).

In the experiments reported here, the author destroyed by electric cautery varying amounts of the cerebral cortex and assayed the effect of this operation on the ability of the domestic fowl to discriminate visual patterns. It was found that the cortex was not essential to vision; a fact in contrast to the results obtained by investigators working with mammalian forms. However, the ability to discriminate in visual learning did vary directly with the amount of cortex destroyed. Birds with large cortical lesions learned more slowly and with less success than did those with small lesions.



LÉSIONS DU PANCRÉAS ET TROUBLES FONCTIONNELS PANCRÉATIQUES. *Diagnostic en Clinique par l'Épreuve à la Sécrétine Purifiée.*

By Marc Bolgert. *Masson et Cie, Paris.* 45 francs. 9 $\frac{1}{2}$  x 6 $\frac{1}{2}$ ; viii + 255; 1935 (paper).

A resumé, with an extensive list of case histories and observations, of the author's work on pancreatic dysfunction as ascertained by the purified secretin test. The first part of the book is confined to technique and interpretation of the test; the second and third parts, to results as obtained in diseases of the pancreas, the liver and gall bladder, digestive tract, colitis, the anemia of Biermer and other ailments. The author concludes that pancreatic disorders are more common in diseases other than those primarily of this organ, than is ordinarily supposed. Fourteen pages of bibliography are included.

DIE HERSTELLUNG UND PRÜFUNG HOMÖOPATHISCHER ARZNEIMITTEL. *Eine Anleitung für das Apothekenlaboratorium.*

By Konrad Schulze. Theodor Steinkopff, Dresden. 4.50 marks. 8½ x 5½; viii + 92; 1936 (paper).

This is a useful guide for the pharmacists who are called upon to prescribe and concoct homeopathic remedies. It is based more or less upon an earlier work by Hahnemann, the *Urgrossvater* of homeopathy; this work being now in its sixth edition. All the latest pill mixing, pulverizing, and drying machines are described. The brochure is probably more valuable for German apothecaries, who have often considerable medical knowledge, than for American pharmacists.



#### GLANDULAR PHYSIOLOGY AND THERAPY. *A Symposium.*

*Prepared under the Auspices of the Council on Pharmacy and Chemistry of the American Medical Association. American Medical Assoc., Chicago. \$2.50. 8½ x 5½; vi + 528; 1935.*

In this series of articles (32) written by specialists, the clinician has at hand authoritative information concerning what is established and what is still theoretical in this important field. The articles originally appeared in the *Journal of the American Medical Association* but have been revised where necessary before publication in book form. Each section is thoroughly documented. The detailed index will be found highly useful. For the general biologist the volume furnishes a valuable summary of endocrinology to date.



HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 449. Methoden der Muskel- und Nervophysiologie.* Containing following articles: *Myothermische Schnellregistrierung mittels des Elektronenröhren-Mikrovoltmeters*, by Edgar Wöhlisch; *Röntgenuntersuchung der Knochen und Gelenke*, by Rudolf Grashey; *Methoden zur Untersuchung der glatten Muskulatur der Lunge*,

by Manfred Kiese; *Eine Kathodenstrahloszillographeneinrichtung für physiologische Zwecke*, by Leon Asher; *Tätigkeitssubstanzen der quergestreiften Muskulatur*, by Gustav Embden and Gerhard Schmidt; *Mikrobestimmungen von Purinsubstanzen in Geweben*, by Gerhard Schmidt.

Urban und Schwarzenberg, Berlin. 14 marks. 10 x 7; 224; 1936 (paper).

The papers in this volume describe new methods of study of nerve muscle physiology. They are mostly concerned with the use of electricity and cathode rays in experimentation. One paper describes a method of registering heat production from muscle by means of a newly invented instrument—*Elektronenröhren-Mikrovoltmeter*. This instrument is considerably more sensitive to thermal changes than others commonly used.



#### BIOCHEMISTRY

##### THE CHEMISTRY OF NATURAL PRODUCTS RELATED TO PHENANTHRENE.

By L. F. Fieser. Reinhold Publishing Co., New York. \$6.50. 9 x 6; xii + 358; 1936.

This is a highly technical discussion and review of the present state of knowledge about the chemistry of a considerable number of substances of great interest to biologists just now. Unless they are also trained organic chemists, however, much of the book will be right over their heads—modern coal tar chemistry is distinctly not a subject that can be lightly taken in one's stride. Phenanthrene is a hydrocarbon isomeric with anthracene. 'Natural products that are derivatives of, or closely related to phenanthrene, include such things as the cancer producing hydrocarbons, the alkaloids of the morphine and aporphine groups, the sterols and bile acids, the sex hormones, the cardiac glycosides and toad poisons, and the saponines including those of the digitalis group. So it is plain that phenanthrene is a juice that the biologist has sooner or later got to know about. Dr. Fieser points the way with great skill and learning; no blame can attach to him if the road itself seems to the biologist to be a tough and rocky one.

ÜBER KATALYTISCHE VERURSACHUNG IM BIOLOGISCHEN GESCHEHEN.

By Alwin Mittasch. Julius Springer, Berlin. 5.70 marks.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; x + 126; 1935 (paper).

This book, written by a chemist, reviews and summarizes what is known, or thought, up to the present time concerning the properties and teleology of the catalytic factors in ferments, enzymes, hormones, vitamins, growth stimulation substances, genes, etc.; their interrelationship and effect on the organism as a whole. The author concludes that:

The totality of the biocatalyzers of an organism appears to be an ordered system of lower teleocausal factors, which are under the authority of the law of life, that is, at the service of the higher aim of the organism (with its higher powers of "Biosfeld") and which are necessary for the chemistry of life throughout all its stages. The biocatalyzer directs and is directed.



PRÉCIS DE CHIMIE. *À l'Usage des Candidats au Certificat d'Études Physiques, Chimiques et Biologiques et à la Licence des Sciences.*

By A. Tian and J. Roche. Masson et Cie, Paris. 80 francs.  $7\frac{1}{2} \times 5\frac{1}{2}$ ; viii + 970; 1935.

A chemistry text intended for students of medicine and biology and written with the express purpose of meeting the new requirements for a doctor's certificate. The book is divided into five parts. Part I is a brief survey of inorganic chemistry and physical chemistry dealing mostly with such general principles as valence, states of equilibrium, electrolysis, etc. Part II deals with hydrogen in great detail. Part III with metals and the various derivative salts, with a concluding section on organic chemistry. Part IV deals with the fatty acid series, and Part V with cyclic structures such as the benzene ring, etc.



REPORTS OF THE BIOCHEMICAL RESEARCH FOUNDATION OF THE FRANKLIN INSTITUTE (Formerly the Cancer Research Laboratories), Vol. III, 1934-1935.

Franklin Institute, Philadelphia.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; collection of reprints.

A bound collection of reprints by various members of the staff of the Foundation. Some 27 of them deal with biochemical subjects related generally to the metabolism of tumors, while 6 are statistical papers on cancer by Dr. F. L. Hoffman.



KOLLOID-FIBEL FÜR MEDIZINER.

By Raphael E. Liesegang. Theodor Steinkopff, Dresden and Leipzig. 1 mark.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; 34; 1936 (paper).

A concise, authoritative summary of the chemical, physical and anatomical properties of the colloids, written primarily for medical men. An index of colloid-chemical terms is appended.



SEX

LA DÉTERMINATION DU SEXE ET L'HÉRÉDITÉ. *Actualités Scientifiques et Industrielles* 258. *Exposés de Biologie. La Cellule Germinale dans l'Ontogénèse et l'Évolution. II.*

By Émile Guyénot. Hermann et Cie, Paris. 20 francs.  $10 \times 6\frac{1}{2}$ ; 79; 1935 (paper).

The distinguished pioneer in *Drosophila* genetics who contributes this brochure to the lively *Actualités* series, gives an interesting, stimulating and critical appraisal of the present theoretical position regarding sex determination. Starting from the point that sex is determined at fertilization, he is of that opinion that as a general rule all individuals inherit the opposed factors of masculinity and femininity which have the tendency to orient the general processes of metabolism in different directions. Sexual differentiation is to be regarded as the resultant of the equilibrium established between these two antagonistic tendencies. The experimental results on environmentally altering the genotypic sex ratio in batrachians are accepted, and interpreted as indicating that what we call factors of sexuality are primarily factors of nutrition—regulators of metabolism—that can be operated in more than one way. Great importance



is attached to the results of Dobzhansky and Schultz showing the multiplicity of feminising factors in the X chromosome of *Drosophila*, because they lend support to the metabolic viewpoint of the author. The problem of intersexuality is discussed. As a document of the "day and fray" this pamphlet will interest the geneticists.



PSYCHOLOGY OF SEX. *A Manual for Students.*

By Havelock Ellis. *Emerson Books, New York.* \$3.00. 8½ x 5½; xii + 377; 1935. The author's reason for writing this book can best be stated in his own words,

... there is need for a small book to serve as a concise introduction to Sex Psychology. Ordinary medical practitioners and students, it is said, are far too overburdened already to be able to master extensive treatises on an additional subject which is not obligatory. The subject of sex in its psychic and social bearings is so central, and of an importance now so widely recognized, if not indeed exaggerated, among the general public, that the medical man of today cannot fail to have it brought before him. He cannot, like his predecessors, conventionally ignore its existence, or feel that its recognition would be resented as impertinent or indecorous. Moreover, a knowledge confined to general anatomy, physiology, and pathology is now altogether inadequate.

The book deals with such topics as the biology of sex, the sexual impulse, homosexuality, marriage, the technique of love, etc., and is beautifully written, as is to be expected from the great master. A bibliography follows each chapter and a short glossary and index follow the text.



ENCYCLOPAEDIA SEXUALIS. *A Comprehensive Encyclopaedia-Dictionary of the Sexual Sciences.*

Edited by Victor Robinson. *Dingwall-Reck, New York.* \$7.50. 9½ x 6½; xx + 819; 1936.

This is a book of 819 pages covering a variety of medical-biological-sociological-legal topics loosely bound together by the ambiguous term "sex." [Reginald, the Office Boy, says it doesn't seem ambiguous to him, especially in the spring]. The material is treated in encyclopaedic fashion with the various topics discussed in

alphabetical order. For each entry there is presented an etymological interpretation of the term in question; a historical sketch of the subject matter where pertinent; an explanation of the subject in the light of contemporary knowledge, and a list of references.

With the individual articles we have no quarrel: most of them, by and large, seem to be creditably written and quite authoritative. Indeed the book prospers by having had the services of some distinguished specialists—Briffault, Lillie, Morgan and others. Our serious quarrel with the book is concerned with the actual need for such a volume at all. It is certainly at best a very loosely integrated production and it seems doubtful that it will fill a real place in the libraries of any but the sexually curious.



PHYSIOLOGY OF LOVE.

By Paolo Mantegazza. *Translated from the Italian by Herbert Alexander. Eugenics Publishing Co., New York.* \$3.00. 9½ x 6½; xviii + 237; 1936.

When the first edition of this book appeared in Italy some sixty years ago, the moralists reacted to it in the same indignant fashion as those of the present day have condemned books on contraception, free love, etc. A generation later this book was considered to have some instructive value. Now it is entirely outmoded. To the reader of modern sex books which reflect a more or less morbid outlook, Mantegazza will appear naïve. Yet, if the translator had avoided such a faithful rendition of the author's redundant and florid style, common in the Italian prose of the period, this book would serve a good purpose. The fact is that Mantegazza was a keen student of human biology, and in this volume he described the range of variation of that complex of psychic and physical manifestation called love, which he saw as a purely biologic phenomenon that transcends morality. A better and modernized translation should make this book popular for the layman who is not interested in pathologic sex problems.

TIME OF OVULATION IN WOMEN. *A Study on the Fertile Period in the Menstrual Cycle.*

By Carl G. Hartman. *The Williams and Wilkins Co., Baltimore.* \$3.00. 7½ x 5½; x + 226; 1936.

The chief purpose of this volume is "to furnish the busy practitioner, . . . , a concise yet comprehensive survey of the essential facts concerning the period of ovulation in women." It is an authoritative treatise. While there still remains much research to be done on this subject the author states that "the opponents of the Safe Period are more and more placed on the defensive as new facts accumulate." The first nine chapters of the book contain brief summaries of the physiological facts concerning germ cells, fertilization, sex cycles, etc. The latter and larger part of the volume deals with the time of ovulation. The work includes figures, tables and graphs, an appendix of 34 notes on the chapter which deals with the age of human embryos, a lengthy bibliography with annotations, and an index.



PROSTITUTION IN THE MODERN WORLD. *A Survey and a Challenge.*

By Gladys M. Hall. *Emerson Books, New York.* \$2.00. 8½ x 5½; 200; 1936.

This is a superficial summary of what little actual information there is regarding the extent and practice of prostitution. The few facts which the author does not quote from well-known publications are derived from sources of dubious value such as "a Harley Street specialist," "a Canadian ex-army captain." Briefly told, the author believes that the "professional" prostitute is now being superseded by the "amateur," and finds the cause of this occupational shift in the "new morality." It is well to remember that similar statements were made at various times in ancient Greece and Rome, during the Renaissance, and at various later periods, but still "professional" and "amateur" prostitution and the institution of monogamous marriage have all along persisted side by side.

THE SINGLE, THE ENGAGED AND THE MARRIED.

By Maurice Chidechel. *Eugenics Publishing Co., New York.* \$2.50. 8 x 5½; xxxiii + 270; 1936.

This is a discussion, couched in a somewhat poetic vein, of the many physiological and psychological problems of sex as viewed through the eyes of the consulting clinician. The book attempts to give information about both normal and abnormal sexual relationships and to suggest practices and procedures calculated to guide the "single, the engaged and the married" into healthful and sane sex habits. It does not differ greatly from the usual run-of-mine sex books and can be read without harm, and with possible enlightenment, by the general public.



BIOMETRY

PROBABILITY AND RANDOM ERRORS.

By W. N. Bond. *Longmans, Green and Co., New York.* \$3.75. 8½ x 5½; viii + 141; 1935.

In this book, primarily addressed to students of physics and chemistry, the author presents the elements of the theory of probability. The order follows that of the standard elementary textbooks, but a judicious selection of examples permits the student to arrive at a real understanding of the field of application of the probability theorems. The subject matter includes sections on permutations and combinations, calculation of the fundamental statistical constants, distribution of errors, probable errors of diverse functions, correlation, curve fitting and periodogram analysis. The numerous and interesting examples make this a useful book especially for the biostatistician who will get some new ideas from them. It is well to note, however, that the method of demonstrating the derivations of some of the formulæ could have been simpler and more straightforward. In common with other textbooks on the subject, the author fails to emphasize at all times the conditions which are necessary in order to obtain significant results by the use of the formulæ.

**DIE VARIABILITÄT DER ORGANISMEN und ihre Normgrenzen. Zugleich ein kurzer Leitfaden der Variationsstatistik.**

By Hans Güntber. Georg Thieme, Leipzig.  
7 marks.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; 132; 1935 (paper).

This monograph discusses statistical methods for measuring variation in human physical, physiologic and mental characteristics. The author introduces the subject with a brief exposition of the principles of genetics, and of genotypic and phenotypic variability. This is followed by a detailed description of the methods of calculating the statistical constants in common use. A number of chapters are dedicated to a summary of the several concepts regarding the limits of "normality." While the subject has been amply treated by numerous biostatisticians, the author's clear presentation will certainly be found useful. The bibliography is adequate.



**AN OUTLINE OF PROBABILITY AND ITS USES.**

By Maurice C. Holmes. Edwards Bros., Ann Arbor, Michigan. \$1.50.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; viii + 119; 1936 (paper).

This is a compendium of the elementary formulae of the theory of probability, their derivations and uses. In a clear and brief manner the author discusses combinations and permutations, Bernoulli and Poisson distributions, the normal probability curve, Bayes' theorem, the chi-square test and correlation coefficients. The examples and problems will be found useful by the student, and special mention should be made of the well chosen list of reference books.



**WIDTH-WEIGHT TABLES. For Boys and Girls from 1 to 16 Years. For Men and Women from 17 to 24 Years.**

By Helen B. Pryor. Stanford University Press, Stanford University, Calif. Single copy, 60 cents; 2-4 copies, 50 cents each; 5-9 copies, 40 cents each; 10 or more copies, 35 cents each.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; 15; 1936 (paper).

These tables are constructed so as to offer

a range of seven normal weights for each height and age depending upon the width of the iliac crest. The recognition of varying bodily habitus types is important and the figures appear to be based on a sufficiently large number of cases to be dependable.



## PSYCHOLOGY AND BEHAVIOR

**AN ENQUIRY INTO PROGNOSIS IN THE NEUROSES.**

By T. A. Ross. The University Press, Cambridge; The Macmillan Co., New York.  
\$3.00.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; ix + 194; 1936.

In the preface, the author justly observes that "knowledge in prognosis has lagged considerably behind other medical knowledge" and that only by statistical surveys can one hope to arrive at an adequate evaluation of therapeutic measures. In this book he discusses the results of the treatment of some 1200 patients of the Cassell Hospital for Functional Disorders, Kent, England. The report is based on all the information obtained from the patients in response to letters of inquiry sent by the author at regular intervals after the patient's discharge from the hospital. Such information is, of course, not always reliable but the author appears to be well aware of this and proceeds with characteristic caution and objectivity in drawing his conclusions. The data, which consist of cases admitted in the hospital from 1921 to 1933, are reported in full and include information regarding sex, age, duration of symptoms, duration of hospitalization, symptoms on admission and state of patient annually since discharge. A number of cases are discussed in detail and used as illustrative examples. The author arrives at conclusions somewhat at variance with those of the Freudian School. He believes that in a number of cases permanent benefit may be obtained with short courses of treatment, by substituting teaching for analysis and without the necessity of exploring the infantile unconscious.

The prognosis is remarkably good for patients with anorexia nervosa but improvement is seldom seen in those with

obsessional compulsive neurosis. The results in traumatic neurosis, he finds, are dependent generally on the nature of financial compensation. For a patient with frank neurosis, the risk of committing suicide or becoming insane is rather small. These and other facts lead the author to affirm that neurosis and psychosis are not different degrees of the same thing.

While from the statistical standpoint the elaboration of the data leaves much to be desired, yet the recognition that this is the method of approach for a determination of prognosis and the author's impartial and detailed discussion of the results, make this book a useful contribution to psychiatry and medicine.



**ESSENTIAL TRAITS OF MENTAL LIFE.** *The Purposes and Principles Underlying the Selection and Measurement of Independent Mental Factors, Together with Computational Tables.*

By Truman L. Kelley. Harvard University Press, Cambridge. \$2.75.  $8\frac{1}{2} \times 5\frac{1}{8}$ ; 145; 1935.

A hand book for students engaged in the analytical study of personality. It is volume 26 in the Harvard Studies in Education. The chapter headings are as follows: A new method of analysis of variables into independent components, Various approaches to the analysis of mental traits, Comparison of components determined by the principal axes method and by the center of gravity method, Social impositions upon the problem of the analysis of mentality, Factors suggested by sundry judgments, and Worksheet and table facilitating the rotation of axes. In this study, a continuation of the author's investigations in the number, nature and relationship of mental traits, is developed a concept of *trait*, "a joint result of original tendencies and surrounding social impositions." The volume contains numerous formulæ, 22 tables, charts (trait ratings by occupational groups, sample ratings for abridged population to show procedure, and revised sample ratings for first trait). There are also given select bibliographies on (a)

Recent literature dealing with the two factor theory and especially with the question of the uniqueness of "g"; (b) Recent discussions of factor analysis techniques; (c) Recent discussions of mental organization; (d) Recent experimental studies using factor analysis techniques. The volume is indexed.



**A REPORT ON TWO EXPERIMENTAL FIRE-WALKS.** *Bulletin II.*

By Harry Price. University of London Council for Psychical Investigation, London.

5 shillings net (Foreign, \$1.25).  $9\frac{1}{2} \times 6$ ; 15 + 20 plates; 1936 (paper).

Practically everyone, at one time or another, has heard stories of native peoples walking, during ceremonial rites, over stones heated to uncomfortable temperatures and apparently suffering no ill effects therefrom. These stories, however, have frequently caused the judicious to express some disbelief as to their authority and wish that an honest, realistic test of them would be forthcoming. It appears that such a report is available in the present paper in which the author describes his observations on two experimental fire-walks conducted by an East Indian in the quiet surroundings of an English countryside. As a result of his researches the author comes to the conclusion, "... that it is possible, for a slightly-built man with chemically unprepared feet, to take four rapid steps on charcoal at 430° Centigrade, without injury to his feet, the average time of contact for each step being approximately half a second. It is hardly necessary to point out that, in rapid walking, the whole of the foot is not put into contact with, or withdrawn from, the ground at one instant, so that *no one portion* of the skin was in contact with the hot embers for as long as half a second. This may therefore be regarded as an upper limit to the time of continuous contact."



**THE MIND OF THE DOG.**

By F. J. J. Buytendijk. Translated by Lilian A. Clars. Houghton Mifflin Co.,

*Boston.* \$2.50. 8 x 5½; 213 + 20 plates; 1936.

This analytical study of the dog's behavior, by a Dutch physiologist in the University of Groningen, is of importance to the behaviorist. It will also interest all dog lovers, although they will sometimes disagree with his conclusions. The author was chiefly occupied in studying the functioning of the organs of sense, impulses, formation of habits and insight in unfamiliar circumstances of life. He did not limit his observations to experimental investigations but closely observed the animals in their natural surroundings. His own tracking experiments agree with those of other workers, namely—that the dog is by no means infallible in following human trails. He is not convinced that a dog really understands our words for, "in my opinion there is scarcely one experiment that is perfectly safe for ascertaining the understanding of words." In habit forming "we have come to realize more and more that in all learning *insight* is also operating and that there is really no action without insight." Numerous experiments of his own and others are cited to make clear his position on this point. A section is devoted to Pavlov's experiments. The volume is well illustrated but is without an index.



**ADULT INTELLIGENCE. A Psychological Study of Test Performances.**

By *Theodore Weisenburg, Anne Roe and Katharine B. McBride.* *The Commonwealth Fund, New York.* \$1.40. 9½ x 6½; xiii + 155 + folding table; 1936.

This is a report of an extensive and thorough study by intelligence testing methods on groups of adult hospital patients, normal as to mentality in the sense of having no discernible mental disease. Among the many interesting details brought out, the authors find that by far the greatest extent of mental development occurs before the twenties, while from that decade through the fifties there is little change, either way by further gains or in the direction of loss. The amount of formal schooling was found to be probably not as important a factor as it is

usually supposed to be. The intelligent man with poor schooling compensates in adult life for his lack. The dullard with a lot of schooling has either forgotten most of it by adult life, or it never really "took" at any time. Sex differences were found to be negligible.

There is a substantial bibliography and an index.



**THE PROBABILITY OF COMMITMENT FOR A MENTAL DISORDER OF ANY KIND BASED ON THE INDIVIDUAL'S FAMILY HISTORY. Monograph Series Number X.**

By *Serge Androp.* *Eugenics Research Association, Cold Spring Harbor, Long Island, N. Y.* 50 cents. 9 x 6; vi + 79; 1935 (paper).

The author presents and summarizes the pedigree charts of 54 families, each of which is characterized by the fact that at least one member of the family, being either feeble-minded, epileptic or insane, has been committed to some institution. The results show that the percentage of commitments is a minimum for the offspring of parents with a negative family history of mental disorders; it is a maximum for those individuals both of whose parents belong to families with a high incidence of these mental disorders.

Before any judgment can be passed regarding the validity and significance of such results, it is necessary that the author revise his method of analysis. It is remarkable that this, a prize winning monograph of the Eugenics Research Association, should have been permitted to appear in print when it contains a major logical error: the assumption that the "probability of commitment for a mental disorder" could be estimated from such selected population.



**GRUNDLAGEN DER RASSENPSYCHOLOGIE.**

By *Egon F. von Bickstedt.* *Ferdinand Enke, Stuttgart.* 5.40 marks (paper); 6.80 marks (cloth); 25 percent reduction outside of Germany. 9 x 5½; 164; 1936. The author believes that a comprehensive

and workable system of race psychology can only be obtained from a thorough study of a wide range of branches of human biology. In this book he reviews critically the more important literature on racial and individual psychology, anthropology, ethnology, human constitution, etc., in an effort to work out some system of methodology which will enable one to differentiate traits which can fundamentally be attributed to race, and race only, from those due rather to environment or other factors. In the current so-called intelligence tests used in an attempt to find mental differences among the races he finds much to be desired. Students of human biology should find this thought-provoking book of interest. It is well documented and there is an index of authors.



DE OMNIBUS REBUS  
ET QUIBUSDEM ALIIS

A WORLD OF CHANCE or *Whence, Whither, and Why?*

By Edward G. Spaulding. The Macmillan Co., New York. \$3.00. 8 x 5½; xxxiii + 293; 1936.

This is a forthright treatise by the distinguished McCosh Professor of Philosophy at Princeton. It has been evident lately that a good many of the Elder Statesmen of biology, whose periodic ejaculates of accumulated and concentrated wisdom in committee rooms keep our science in safe channels, were beginning to be vaguely disturbed by all this loose talk of the physicists about the "principle (God save us!) of indeterminism." Nicely brought up intellectually, they dislike such slightly blasphemous even if playful monkey business with the Sacred Things, like cause and effect. Youth tends to ebullience, of course, but these are serious times fraught with such dangers that the boat had better not be rocked. Indeed (just between ourselves and don't quote me), just as Mr. Roosevelt and Mr. Farley are taking steps to implement the obvious deduction that this would be a better world if it contained no Republicans, perhaps a hint in the right place might lead

to a safer and saner allotment of funds to right-minded physicists, and then all this nonsense would be soon stopped.

It is too bad, but *A World of Chance* is destined to give the old dears a dreadful jolt. For Dr. Spaulding not merely grasps the sprightly bullock of indeterminism firmly by the horns, but hangs a lei of high-toned mathematical logic around its neck, suspends a halo above its head, and by the clever exhibition of various sorts of hormone therapy does his level best to transform this mischievous he-devil into a Sacred Cow of Scientific Respectability. To the queries of the subtitle *Whence, Whither, and Why?* the answers, in clarion tones are: From no Source, To no End, and For no Reason. So far from indeterminism perhaps occasionally playing a small trick on earnest thinkers, it is the whole works.

Far be it from us to say whether the book establishes its thesis. So great is the influence of our lightest word that to do so might deter some of our customers from reading it, and thus deprive them of the pleasure thereby to be gained. It must suffice to say that the argument is shrewd and clever. The terminology of mathematical logic in which a good part of it is couched is a bit forbidding, and undoubtedly—and also unfortunately—takes the book right out of the realm of easy or rapid reading. But it is a book that had best not be neglected.



WHY KEEP THEM ALIVE?

By Paul de Kruif, in collaboration with Rhea de Kruif. Harcourt, Brace and Co., New York. \$3.00. 8½ x 5½; 293; 1936.

In a sentence, this, the latest book by Paul de Kruif, could be characterized as follows: We know a lot about the technique of reducing child mortality, morbidity and general suffering—isn't it just terrible that all that is known is not universally practised? In other words, why is any child ever allowed to suffer when medical science is so able to help them? The answer suggested, mainly but not entirely by indirection, is that when the present economic and social system shall have been overset and all the fit and provident folk

now able to take care of themselves in an ungentle world have been forcibly put under the domination of the less fit, who are so to be pitied now because they do not get all of the best the world has to offer, then all will be well or at the very least a great deal better. Such diverse subject matter as the treatment of burns, hunger and the problem of child nutrition, tuberculosis, *and* the Dionne quintuplets is utilized to pile horror on horror.

The book is in essence a piece of exag-

gerated emotional propaganda for the extension of public health services. The further development and extension of public health is wholly to be desired, and is in fact occurring all the time by normal processes of social evolution. Past experience has demonstrated however that its orderly progress has not been helped, but rather hampered, by emotional overstatements of the case before the court of Common Sense, J., sitting with Humanity, J. and Decency, J.



# THE QUARTERLY REVIEW of BIOLOGY



## SEXUAL PHOTOPERIODICITY

By THOMAS HUME BISSONNETTE

*Trinity College, Hartford, Connecticut, and Marine Biological Laboratory,  
Woods Hole, Massachusetts*

### INTRODUCTION

IT IS now comparatively well known that seasonal sexual reproduction in some plants and animals is conditioned to greater or less degree by the relative lengths of day and night, by the intensity of illumination, and, in some cases, even by the color or wavelength of the light used to vary the length of day. This is not equally true of all plants nor of all animals. Other factors of the environment and hereditary or constitutional factors also influence the type and time of the manifestations of sexual activity.

It is proposed to discuss these phenomena briefly in attempting to see (1) how far one may go in classifying plants and animals on the basis of the relation of their sexual reproductive cycles to light in its various aspects, and (2) how the facts concerning these relations have been ascertained. Special emphasis will be laid upon the recent studies on animals; but the situation in plants, which is perhaps more completely known, will be reviewed briefly first.

### SEXUAL PHOTOPERIODISM IN PLANTS

As early as 1890, Curtele (7) found that light intensity was a factor related to blooming and fruiting in some plant species, that some failed to bloom in very diffuse light and that the number of blossoms and the size of fruits were smaller in diffuse than in bright light. Vöchting (43) confirmed these findings and showed that under weak illumination the formation of flowers in numerous plants was either prevented or rendered imperfect and that blooming was correlated with the activities of leaves. Schimper (40) pointed out that "shade plants" bloom on a lower minimum intensity of light than do "sun plants," yet "shade plants" produce fewer flowers.

Even forty years ago, therefore, it had begun to be suspected (1) that there was some relation between length of day or type of illumination and sexual activity; (2) that sexual cycles or activities were not entirely matters of internal rhythm fixed by hereditary constitution and entirely independent of environment; (3) that temperature cycles might not be the



major factors conditioning seasonal reproductive cycles.

Klebs (24) was one of the first to investigate this problem experimentally in an attempt to modify the blooming time of *Sempervivum*, a plant which normally blooms in June. By increasing its daily period of illumination he induced it to bloom in winter.

But it remained for Garner and Allard (13, 14, 15, 16, 17, 18, 19), Adams (1, 2, 3), and others (4, 12, 21, 28, 9, 42, 23, 29, 31) to make a broad systematic study experimentally of the relation of onset of blooming, including sexual reproduction, in many plants to the relative lengths of day and night and to changes in this relationship. Garner and Allard (13) laid the foundation for and formulated a classification of flowering plants on this basis. They coined the word "photoperiodism" for the response of plants to changes in relative lengths of day and night by beginning to bloom, or to their exhibition of "sexual" photoperiodicity. They reached the conclusion, which subsequent research has continued to support, that flowering plants fall into three classes so far as photoperiodism is concerned;—(1) Short-day plants, which begin to bloom when days are shorter than 12 hours long or when, naturally or artificially, they become shorter than a critical or usual length; (2) Long-day plants, which come into bloom when days lengthen or become longer than a critical length in relation to nights; (3) Ever-blooming or indifferent plants, which complete their reproduction without definite relation to the day-night ratio or within very broad limits of day-length (23, 31).

Wann (44) tested the photoperiodism of *Marchantia polymorpha*, a bryophytic non-flowering plant, and found that its gametophyte is a long-day plant in its sexual reproduction.

Garner and Allard (13, 15) and Kellerman (23) show that this response is quite definitely localized. Even the top and bottom thirds of a plant, like late-blooming *Cosmos*, can be brought into blooming by experimental alterations of their periods of exposure to light while the middle third is kept growing vegetatively without flowering, and *vice versa*. They found that very weak light from electric bulbs, as low as one one-thousandth of the intensity of sunlight and almost lacking ultra-violet and some other constituent wave-lengths of sunlight, was enough to bring on flowering in some long-day plants. Wave-length did not seem to matter much in this response, though it does for growth (32) and germination (11). Flammarion, about 1898 (10) (cited from Garner and Allard (13)), however, had found that some plants bloomed earlier in red light than in white. The lower limits of effective intensity do not seem to have been determined yet. Garner and Allard (23) found that alternate single hours of light and darkness were not equivalent to twelve hours of light followed by twelve of darkness. But a period of two hours of darkness in the middle of the twelve hour period of light did not appreciably lessen the response, though the light time per day was thereby reduced to ten hours. So it takes some time for the response to get under way, and the momentum of the reaction bridges a two-hour gap of darkness.

The fundamental chemical internal changes in the plants upon which the inception of reproductive activity directly depends have not yet been determined beyond controversy. Some have suggested changes in sugar concentration (24), in H-ion concentration of the sap (20) or in carbohydrate-nitrogen ratio (22, 27).

The relations of sexual photoperiodism to other environmental factors,—tempera-

ture, humidity, and available carbon-dioxide,—have been studied. It has been shown that response to changes of period of light can be modified by changes in these other factors in some cases (8, 22, 5, 6, 29, 41). If the light period is suitable for a particular plant, it will bloom as quickly as climatic conditions permit; but if the light period is not suitable, weather changes cannot cause flowering (23).

Since 1919, Schaffner (34, 35, 36, 37, 38, 39), Richey and Sprague (33) and others have been finding that relative length of day and intensity of light influence the expression of maleness or femaleness in some plants such as hemp, maize, Jack-in-the-pulpit and others, and that this expression may be modified or even reversed experimentally by altering the length and intensity of daily illumination for these plants. Loehwing (25) has shown that male plants of long-day spinach and of short-day hemp have higher percentages of iron, magnesium and sugar, more soluble sap constituents, and greater oxidase activity of tissue fluids than female plants. This is in agreement with Manoilov's reactions (26) and with those of others.

#### SEXUAL PHOTOPERIODICITY IN ANIMALS

Studies on sexual photoperiodicity in animals will be treated more or less chronologically, though the early studies were independent of each other.

In 1698, Martin (103) reported "The inhabitants observed that when the April moon goes far in May the fowls (referring to sea birds) are ten to twelve days later in laying their eggs, than ordinarily they use to be." This suggested an influence of moonlight as well as sunlight on the reproductive periodicity of wild fowl.

In 1907, on theoretical grounds, Sharpey-Schafer (120) suggested that

the regularity with which migration occurs (in birds) indicates that the exciting cause must be regular. There is no yearly change outside the equatorial zone that occurs so regularly in point of time as the change in the duration of daylight. On this ground this may well be considered a determining factor in migration, and it has the advantage over other suggested factors that it applies to the northerly as well as to the southerly movement.

He said further, however, "that it is the result of developmental changes in the sexual organs is improbable." This was because the sex-glands of spring migrants were still about as small as in autumn.

Keeble (94) described the peculiar cyclic behavior and breeding activities of two worms of the genus *Concoluta*. Egg-laying reaches its maximum when the animals are exposed to only six hours of light each day, at intervals of two weeks, in relation to spring tides or under experimental conditions. They, therefore, correspond to short-day plants. There are many other cases of such periodic behavior among aquatic invertebrate animals; but it is open to question whether they are true cases of sexual photoperiodicity. So they are not included here.

Marcovitch (98) studied plant lice or aphids in which sexual individuals usually appear in autumn. It was believed that falling temperature was the cause of their appearance. He showed, however, that the much more marked and regular shortening of the days was the major environmental factor concerned. The strawberry root louse (*Aphis forbesi*) normally produces sexual individuals in November and the eggs hatch in February. By subjecting very young individuals to days of about eight hours soon after hatching, he induced the appearance of sexual individuals on May 7 and egg-laying on May 22. Temperature was not a factor. Migration of the aphids in autumn, which precedes the appearance of sexual individuals, was also conditioned by relative

length of day in several species. Males and sexual females were obtained in June in high temperatures by keeping them and their host plants exposed to short days for about seven weeks. He also found that the rosy apple aphid (*Aphis sorbi*), in which migrants may occur in any generation after the third in spring, responds to increasing length of day by producing migrant individuals. They would, therefore, correspond to long-day plants, while the others mentioned above would correspond to short-day ones.

Eifrig (81), on purely theoretical grounds, suggested that bird migration is a response to change in length of day but is not dependent on sex-gland changes.

#### *Experimental studies on birds*

Before 1925, Professor Rowan (110, 111, 112, 113, 114, 115, 116) of the University of Alberta, Edmonton, began his studies on the relation of changes in length of day to migration of the snow bird (*Junco hiemalis*). In Edmonton, the temperature in winter falls below  $-50^{\circ}\text{F}$ . By a series of experiments carried out in open cages in winter, he showed that reversing the daylight curve in autumn and winter, by adding electric light after nightfall in increasing periods, would cause the sex-glands of juncos, canaries, and crows to enlarge and produce sperms in winter instead of at the normal breeding season in April or May. In juncos and crows, this enlargement was correlated with the tendency to migrate north. Southward migration was correlated with regression or diminution of sex-gland size and activity, which could be brought about by shortening their daily exposure to light. Weak light from electric bulbs was sufficient to bring about the breeding condition four or more times a year if added after nightfall for a time and then withheld. His interest was primarily

with the relation of migration to cyclic seasonal changes in length of day. He concluded that migration is dependent on cyclic changes in the sex-glands, and called this group of responses "photoperiodism" after Garner and Allard (13). Rowan has suggested, and his evidence, though incomplete, in general supports the idea, that juncos and crows migrate northward toward longer days when their sex-organs are increasing in activity, and southward toward longer days when the organs are regressing or have regressed to a certain stage in autumn as the result of shortening days in the northern regions.

We are not interested primarily in the migration problem, but in the reaction of the sex-glands to changes in length of day. Nevertheless, on the basis of our studies on starlings and ferrets and of some of Rowan's own data on castrate crows and migration, it may not be too foolhardy to suggest that possibly the migration urge originates beyond the sex-glands and depends on states of the activities of the anterior hypophysis. Evidence is accumulating to show that the hypophysis is responsive to light stimuli based on length of day in some animals (89, 90, 91, 92, 59, 63, 64, 67, 68). It is known to control the activities of the sex-glands and, through them, the accessory sexual apparatus and behavior (76, 77, 78, 87, 88, 121, 122, 117, 118). It is, perhaps, not going too far to credit it with the migration urge also as an early phase of the drive toward mating reactions in spring, and as a phase of the reaction from it in autumn. The bases for this suggestion may be more evident after later studies have been described.

Unfortunately Rowan (113) on the basis of a very limited and, therefore, misleading experiment, using increased exercise with reduced lighting periods on some birds already well advanced in sex-

gland activation in March, came to the conclusion, and still maintains, that "It would thus appear that radiation may be definitely eliminated and that increasing exercise suggests itself as being responsible for the recrudescence of the organs of the junco. The extra consumption of food for reasons discussed elsewhere is of questionable significance." As will appear later, in starlings and some other forms at least, it is the increase in periods of light, as such, that modifies the sexual cycle, and *not* the increasing exercise. The results of work by Bissonnette and others cited above support his statement about the relative unimportance of amount of food consumed, above the minimum to prevent inanition. But it is quite evident that quality or variety of food does act as a limiting factor, and plays an even more important rôle in some cases. Longer feeding periods or shorter night periods without feeding have been looked upon by poultrymen as the cause of the increased laying of fowls in autumn and winter when they are subjected to "night lighting." But experimental studies on birds by Rowan, Cole (73), Miyazaki (105, 106), Benoit (53), myself (54-73 inclusive) and others (86) and similar studies on sexual photoperiodicity in mammals (47, 48, 50, 51, 52, 61, 63, 65, 67, 69) and Amphibia (119, 127) rather indicate that the larger consumption of food is the result of increased reproductive or sexual activity, instead of its cause.

Between 1926 and 1928 Bissonnette and Chapnick (70) and Bissonnette (54, 55) and since that time, Bissonnette and Zujko (74) studied the normal sexual cycle of the European starling (*Sturnus vulgaris*), a bird which migrates only very little in this country. At Hartford, Connecticut, they form great flocks in autumn and winter and roost around buildings and sometimes in trees in the city at night

and spend the day scouring the country for insects and other food. Birds were killed for study of their sex-glands at approximately fortnightly intervals. The changes were checked for a second year and an attempt was made to find some correlation between the observed changes in the sex-organs and some regularly changing factor in the environment such as temperature, barometric pressure, daily hours of daylight, etc. It was impossible to ascertain types of food or its amount at the various times or the daily intensity of illumination, since the birds were taken from nature and had free range.

Of all the environmental variables tested over the period of study, daily hours of daylight increased and decreased uniformly from year to year in close correlation with the changes of the sex-glands occurring at the same dates each year. Temperature and barometric pressure varied very irregularly and increase in testis size and activity appeared to bear no consistent relation to them (70).

An experimental study was therefore begun to ascertain whether or not there is any close correlation of the ebb and flow of the tides of sex-gland activity with the waxing and waning of daily periods of light. Rowan's theory (113) that cycles of daily hours of exercise rather than hours of light were the fundamental cause of sexual cycles did not seem to be demonstrated beyond question by his very limited experiment nor to be the only explanation compatible with his data. So it was tested along with the effectiveness of increased lighting without forced exercise, against controls without added light or exercise.

Apparatus modelled after Rowan's, but with improvements to increase its effectiveness, was used to disturb the birds in one cage from their roost and the floor every 20 seconds for definite periods after

nightfall increasing up to seven hours per night. Birds in another cage were subjected for equal periods each night to light from 60-watt bulbs. Those in another cage were not lighted or exercised after nightfall. Experiments were carried out from December to April inclusive.

Added exercise periods without added light, were not only ineffective to induce activity of the sex-glands, but tended to reduce both the sizes of the testes and their germ-cell activity. Added light, on the contrary, proved to be a very potent stimulant for activation of the sex-glands of the starling (56).

By modifying the experimental method and the previous sexual condition of the birds used it was found that increasing exercise periods led to a lag in onset of changes in the testes induced by changes in day-length, whether these changes consisted of increase of activity induced by increasing exposures to light or of decreasing activity or regression consequent from reduced lighting. Increased periods of exercise merely fixed the trend of change in testes operating before changes of lighting, of exercise, or of both occurred. The delay in activation due to this lag or prolonged refractory period was usually more than made up for later by increased acceleration of changes of the testes, once the changes had begun (56).

Exposures to light after sundown, up to six or seven hours per night, led to complete spermatogenesis and maximum size of the testes (sometimes greater than the natural spring maximum) in from four to six weeks at any time between November and May. Controls subject only to short daily periods of light, like those of winter, did not come into activity even in April, May or June, when, in nature, the testes are at maximum size and activity, or past it. The testes of birds on forced exercise periods added to short winter-

like daily periods of light became smaller and less active in spermatogenesis than those of controls without added periods of light or exercise. The state of activity of the testes (and of ovaries as judged by gross inspection at autopsy) could be modified at will in either direction, within the limits of their natural changes, by increasing or decreasing their daily periods of illumination. Some birds could also be kept a month or more in a condition of partial regression by holding constant their daily periods of light and exercise, once the increase or decrease of activity had been stopped by the constant light period (56).

Further studies (57, 58, 71, 72, 73) aided by grants from the National Research Council, Committee for Research in Problems of Sex, showed that the rate or degree of stimulation of testis activity varies with the intensity of illumination used, since birds under a 10-watt bulb were slower to reach maximum activity than those under a 15-watt bulb, and these again than those under a 25-watt bulb, and so on. Birds with added periods of both light and exercise were slower to begin activity, but later overtook those with added light of similar intensity alone. The optimum intensity or duration of the daily period have not yet been determined.

The degree of stimulation for starlings depended also on the color or wave-length of visible light used (58, 71). Red was found to be very highly stimulating. Green of equal luminous intensity, used for the same daily periods, was not stimulating, but was rather inhibitory to activities of testes and ovaries in the great majority of cases. White light was less effective than red of the same luminous intensity, probably because of smaller content of red or other stimulating rays. With much lower luminous intensity,

violet light was apparently slightly inhibitory. This difference in the effect of red, green, white and violet lights was not due to heat or total energy intensity but to apparent wave-length specificity.

That this apparent specificity of wave-length in the visible spectrum for sex-gland stimulation is not found in all animals has been shown by Marshall and Bowden (102). They found all wave-lengths tested, between near infra-red and near ultra-violet, to be effective in activating the sex-organs of ferrets. Within these limits, intensity and duration of light were the most important factors. Beyond these limits of wave-length, radiations were not effective.

In starlings, daily period, intensity, and wave-length of light reaching the birds are factors in controlling the seasonal sexual cycle when diet is adequate, varied, and rich in vitamins, proteins, salts and fats. On a "middlings mash" diet, however, without added vitamins, proteins, salts or fats, even red light of higher intensity than that used in the preceding experiments was almost completely prevented from inducing any increase in sexual activity in starlings in January (64). So improper food, even in sufficient quantity, acts as a limiting factor which may prevent even highly stimulating exposures to light from inducing sexual activity, or greatly reduce its effectiveness.

No mating or egg-laying in starlings was observed under these experimental conditions, even in birds brought to complete sexual maturity, as judged by histological criteria. Mating and laying in these wild birds seem to be controlled by factors outside the crowded conditions in these experiments and not by mere gametogenic fitness for breeding, as judged histologically only (63, 64). Professor L. J. Cole (75), however, by similar methods, induced mourning doves, which do not

breed naturally in autumn and winter, to mate and produce viable eggs in winter. These doves will breed in captivity in their proper season without the added light stimulation.

With starlings a maximum effect and consistent results were obtained by giving large and immediate increases in daily periods of light with electric light, rather than by gradually increasing periods, even in autumn when daily periods of daylight decrease. Filtered red light of 1.7 foot candles luminous intensity, acting for six hours each night from the start, after nine and a half hours of daylight gradually decreasing with the season in a basement room, induced complete spermatogenesis in 23 days in December and January. Other combinations including red light did it in 18 days (56, 57, 58, 71, 72, 73).

Normally testis regression in starlings apparently occurs invariably before June 8 or 15, for no birds killed on those dates or later had remained at complete spermatogenesis (55). But the daily periods of light are still increasing slowly up to June 21, in both duration and intensity. Experimental studies indicated that, even with the most potent schedules of lighting used, birds invariably passed the climax of testis activity and size after a time and underwent regression. This regression was more or less independent of the proportions of ultra-violet or green in the light used. It was due to a "throwing out of gear" of some part of the sexual or reproductive mechanism. Even with the most stimulating exposures to light used, it was impossible to maintain maximum testis size and activity beyond a certain period which varied with the times occupied by the activation phases of the cycle. The time occupied by any phase of the sexual cycle appeared to bear an inverse relation to the effectiveness of the light stimulus used. Animals quickly brought

into maximum activity remained in complete activity for a shorter time than those more slowly activated (57, 58, 71, 72). This loss of activity, even on high stimulation, occurs in male and female ferrets also (65, 67, 68). Long continued injections of gonadotropic hormones from the anterior pituitary and from "pregnancy urine" have shown this same sort of failure to maintain activity of the sex-glands and secondary sexual characteristics in rats, rabbits and even in monkeys according to Collip and his associates and to Meyer and Gustus (49, 76, 77, 78, 117, 118, 104).

A grant from the Grants-in-Aid Committee of the National Research Council and a sabbatical leave from Trinity enabled me to study at Cambridge University in 1931-2 to extend these studies on the starlings and to begin similar studies on ferrets. These mammals have a seasonal sexual cycle or periodicity like that of the starling.

An unsuccessful attempt was made to determine whether the light affected the starlings through the head. Light-tight hoods were used upon half the birds in a cage while added exposures to light were made. But all the birds in the cage died as the result of the handling of the birds to put on and take off the hoods, and nothing came of it. However, the experiment on defective diet, described above, was carried through and its results were taken to show that, if either the light exposures or the diet be too restricted, sex-gland activation fails to occur. This may throw some light upon the sexual cycles and reactions of tropical birds as these may be related to changes of food and of light. This has been discussed in previous papers (61, 63, 64).

Last December, Benoit (53) showed that ducks respond to increased length of day by increased sex-gland activity during

their quiescent period. He found that the eyes were the receptors of the light stimulus. Ducks with their eyes covered but the rest of the body exposed were not affected by increased length of day; while those with bodies covered and eyes exposed were. We have had similar experience with hooded ferrets (67, 68, 69, and unpublished data).

Miyazaki (105, 106) has shown that a green bird of Japan called the mejiro (*Zosterops palpebrosa japonica*) can be brought into sexual activity at least three times each year, instead of once as in nature, by the practise of "yogai." This consists of adding illumination at night. It has been practiced for many generations in Japan to induce early mating-song in these birds. Reduction of daily light period led to moulting.

In a private communication, Dr. Scott of Kansas State College of Agriculture tells me that he has induced mating and laying with turkeys in January instead of March by night-lighting but was unable to get any effect if the lighting was merely given during the daytime as additional intensity. Neither was he able to obtain any effects upon Guinea fowl with night lights. This is an interesting difference between the turkey and the Guinea fowl. The former is native to the temperate zone and has been subject to natural selection for seasonal breeding in spring, probably on the basis of reaction to light cycles, for countless generations, in which those not properly related to the season were eliminated by adverse climatic conditions at a critical period in their early lives. The Guinea fowl was native to the tropics where such selection would be absent, much less rigorous, or based upon some other environmental factor.

For many years domestic fowl have been induced to increase egg-production in autumn and winter by "night-lighting"

(125). The first account of such use of night-lights with poultry is traceable to a Spanish book of 1802. But Waldorf was the first to use this method in this country in 1895, according to Lippincott and Card (95). By 1920 almost all commercial poultrymen in some states were using it. It is known now that fowl may be bred to high autumn and winter production without the aid of night lighting. In hens the response to it is evident in ten to twelve days.

Dr. Callenbach of Pennsylvania State College tells me in a private communication that he has found that the temperature of the brooder in which chicks are raised can make a difference in the time at which pullets reach sexual maturity and lay their first eggs, when lighting conditions are constant.

As the studies on starlings stand, both light and diet appear to be factors in the control of sexual cycles,—light more than diet. Other factors not yet tested may also modify the response.

#### *Experimental studies on mammals*

The normal seasonal sexual cycles of male (45, 46) and female ferrets (83, 99) have been very thoroughly studied. The animals come into sexual activity once a year and have a long period of sexual quiescence. Males complete spermatogenesis between February 12 and 20 and become aspermic or unable to breed in late August. Females come into oestrus or breeding condition in March or early April and remain in heat when unmated till late August. Ovulation occurs only after the orgasm of copulation and between 34 and 36 hours after the beginning of copulation according to my experience, 30-40 hours according to others using larger numbers (99, 83, 84, 85, 87, 88). Pregnancy and pseudo-pregnancy are of

equal length, about 42 days, and females usually come into oestrus a second time if either suckling or pseudo-pregnancy terminates before the end of August. The animals are easily kept in the laboratory and often become quite tame and tractable. One great advantage offered by ferrets for studies of this kind is that, when oestrus approaches, the vulva or margin of the opening of the female reproductive passages begins to swell and finally reaches the diameter of about three-quarters of an inch or less when the receptive stage of oestrus comes on. This obviates the necessity of taking smears of the vagina walls and makes it plain when oestrus occurs. The swelling subsides at the beginning of anoestrus and disappears entirely during the long winter season from August onward, or when pregnancy or pseudo-pregnancy follows copulation.

In my work with these animals only small numbers have been used in any one experiment. But variations in experiments and their results have served as checks on each other and the results have been consistent throughout and with those of others for the most part, though my conclusions and theirs have not always agreed in detail.

Before the experiments to be described below (59), it was held by various students that the sexual cycle of the ferret was not amenable to control by changes in time of illumination or the light to which it was exposed (88, 126). A ferret had not been known to come into oestrus or breed in the northern hemisphere between September and February inclusive, except as the result of injections of gonadotropic hormones from the anterior hypophysis or pregnancy urine. Males did not even become fertile under these treatments (88). Nor did either sex after treatments with small doses of ultra-violet (88).



On October 12, three females and three males were placed in six rabbit cages in two vertical rows, females in one and males in the other, facing a large double window left partly open at all times. A 200-watt electric light bulb was fastened in a clamp at such height and distance from the cages that it threw light directly into all six, from just above the floor-level of the upper cages and to the back of the floor of the lowest. This triangulation kept the distance constant and the animals always in direct light when light was on. Luminous intensity in the cages under experimental light varied from about 4.9 foot candles at the back of the lowest cages to about 14.1 at the front of the upper ones. Light was turned on for six hours each night after nightfall by a time switch, in accordance with the finding for starlings that immediate maximum increase of exposure to light would give best results. These experimental animals were not given nest boxes to sleep in, but only scanty shavings to make shallow beds and to keep the cages dry. This prevented them from keeping as warm as controls, kept in a similar room across the hall with nest boxes and somewhat more general daylight because of larger window area. Windows in both rooms were kept open at all times and temperatures varied with that outside with the season. Drafts from the windows swept across the space between the lamp and the cages. Food was uniform for all animals.

Ferrets spend most of their time curled up in sleep with their heads in the middle of the circle formed by the body, except when sexually active, when they run back and forward across the fronts of the cages more than during anoestrus. This position of the head had a slight effect on rate of activation in different cages under the conditions of these experiments because

the heads were somewhat shielded from direct horizontal light but not from oblique or vertical light (59).

Before November 23 (42 days) two of the females were in complete oestrus; the third lagged till she was prevented from hiding her head in shavings on December 1. She came into oestrus on December 20. Controls showed no signs of oestrus till the regular time in March.

Two of the experimental males died from abscess in the head and from cause unknown on November 18 and 25 after 37 and 44 days of added lighting respectively. In spite of these fatal illnesses, their testes were enlarged and had increased in activity. The epididymis of one was modified toward the breeding condition. They were compared with those of a male purchased from a dealer and killed on December 12, as control. The testes of the surviving male increased in size, descended into the bottom of the scrotum and his scrotal hair became scanty. His libido became that of the breeding animal and his epididymis also. He mated successfully with the oestrous females on December 11, 12, and 21, for the characteristic long periods (10 minutes to 3 hours for ferrets) and the females were all pseudo-pregnant and underwent the changes incidental to that condition. The male was killed for study on December 22, the day following his last copulation, which lasted one hour and forty minutes. No sperms were found in the vagina of any of the females. His testes showed completely active interstitial cells correlated with an epididymis in full breeding condition; but the germ-cells in the tubules had not multiplied beyond the secondary spermatocyte stages, though they showed some evidence of an initial stimulation, followed by slow regression before he was killed. Control males had no sexual

interest in these females though the females were in complete oestrus. A male transferred from control to experimental light in November showed strong mating reactions even on December 12, though his testes were only slightly enlarged and he was not producing sperms (59).

Various modifications of the initial experiment were carried out, such as keeping the days constant in length with curtains, shortening the periods of daily light or reducing its intensity and so forth. Hoods have been used which covered the eyes and head, others which covered the head but not the eyes. Hypophyses have been removed from some ferrets and optic nerves severed in others. Added light periods have been tried on all such animals, with controls, and animals have been subjected to increasing periods of light for long periods and carried over for more than a year and a half to follow the late and after effects of the exposures to light (69).

Even in the early experiments the method used was fully effective on females. Ovulations followed copulations with light stimulated males that were still aspermic. It was thought that males were less susceptible than females to changes in length of day. This has turned out to be an incorrect conclusion in the light of experiments in which gradual increases in the length of day were made. Males are apparently more sensitive to changes in length of day than females and react more quickly to lessening day-length (67, 69). This accounts for the results in the first experiment in which the slowly decreasing daylight periods after the initial artificial increase in total time of light caused regression after an initial activation. This method brought females into complete oestrus and permitted

them to continue in heat for some time (69).

Females kept at a constant daily daylight period in spring by the use of curtains came into a delayed oestrus on a constant seven and a half hour light period, as the result of increasing intensity of the daylight in April and May and of some light filtering around the edges of the curtain into the cages during that part of the day when the cages were curtained. But they went out of oestrus when moved into cages into which this additional light did not penetrate. Females brought into oestrus and kept in that condition for some time by light periods increasing up to 18 hours per day went into anoestrus when the periods of light were reduced to 16 hours as well as when reduced to 8 hours. So it was concluded that the previous light history of an animal or the light to which it had become accommodated or temporarily adapted, and its endocrine or physiological condition determines the effect of any given length of day. Increasing day-length induced oestrus in animals not already in oestrus; decreasing it induced anoestrus in those in oestrus or delayed oestrus in those already activated to begin activity of the sex-glands. But a good start into activation carried females into oestrus even when light-periods were slowly reduced after the initial impulse (69).

After comparing these results with results following treatment with gonadotropic hormones from the anterior hypophysis, we have suggested that the anterior hypophysis is stimulated by the increase in length of day and in its turn stimulates the sex-glands which control the accessory sex-organs and behavior (59, 67). This is in some respects like the effect of light and dark surroundings on various fish, reptiles, and crustaceans studied by Professor G. H. Parker and

others, in which humoral agents mediate the changes (108, 109).

Hill and Parkes (91, 92) have confirmed our results in the induction of oestrus in the anoestrous period in ferrets. They have shown that hypophysectomy obliterates sexual cycles and prevents increased lighting from inducing oestrus in ferrets, and we have confirmed this. They have shown that both male and female ferrets come into sexual activity and breed, if, after normally increasing days to January 24, they are confined in total darkness for 23½ hours or more per day, though the coming of oestrus is delayed in females, at least. One female bred twice in the five and a half months of the extremely short periods of light. Possibly the initial stimulus of 34 lengthening days was enough to carry the animals into complete sexual activity, though more slowly after the reduction of periods of light (102). The males were already within 12 to 14 days of the coming of sperms on the normal cycle (46). If this is the case these results are consistent with ours and with those of Marshall and Bowden (102).

Our first experiments with males did not induce complete sperm production in autumn or winter. But by increasing the daily period of light gradually up to seven or eight hours per night from October 2 onward with males over one year old, instead of with those not yet fully grown, we have succeeded. Sperms have been produced as early as November 7 [the low point in the normal cycle (45)] and copious ejaculations of sperms in matings on November 26 (65). Allanson, Rowlands and Parkes (47) obtained fertile matings on December 29, from a male, by increased length of day followed by injection of urine of pregnancy extract. Some of their males came into spermatogenesis

in January on increased lighting periods alone. But pregnancy urine usually stimulates only the interstitial cells, and not the germ-cells which are stimulated by the hormones of urine from castrates and from persons past the menopause (121, 122). So it is doubtful if their injections hastened the spermatogenesis.

We have good evidence that there are two factors affecting the testis, differentially stimulated as to their production by the increase in length of day. The factor most quickly stimulated in ferrets by light acts on the interstitials and these activate the accessory organs and libido. This factor also continues to act longer than the second one. This second one acts upon the germ-cells and induces spermatogenesis. It is more susceptible to reduction of day and, in the ferret, is the first to cease to be effective when regression of the testis begins, independently of the increasing length of day. Both factors, however, fail to remain effective beyond a certain period and regression sets in, in spite of lengthening days, just as in the starling (59, 65, 67, 68, 69). Similar changes occur in long-continued administration of gonadotropic hormones from the anterior hypophysis and urine of pregnancy (49, 76, 77, 78, 117, 118, 104) with rats, rabbits and monkeys. The hypophyses of these male ferrets were modified histologically and cytologically by the changes in length of day in correlation with the changes in the sex-glands (65, 67).

Baker and Ranson (50, 51, 52), who started work on mammals before I did, have shown that, for field mice, length of day, type of food, and latitude are all factors in controlling sexual cycles. Allanson and Deanesly (48) have shown that hedgehogs respond to length of day, temperature and hormone injections.

These two species are therefore less stable than ferrets in their sex mechanisms and sensitive to more factors in the environment. Even the clawed toad of South Africa (*Xenopus laevis*) is affected by reduction of daily duration and intensity of light and its sex-glands undergo involution in captivity with reduced light (127, 119).

On the contrary, the Guinea pig shows practically no response to changes in length of day by changes in its sexual cycles. The time of night at which most females first show receptivity toward males is slightly shifted; but cycles are otherwise unaffected (80). The 13-lined ground squirrel (*Citellus tridecemlineatus*) shows no modification of its sexual cycle induced by changes in relation to light, according to Moore and his associates (107, 123, 124) and Johnson and Wade (93). Among fish, the stickleback responds to changes in temperature but not to those of light (79). Doubtless many other animals fall in these classes.

Most sheep come into oestrus and breed in autumn on a falling length of day and so come to drop their lambs in spring. Some breeds, however, appear to have two cycles of breeding times each year and are sexually active in both spring and fall (100). This is true also of other species, which, therefore, correspond somewhat to short-day plants. Ferrets, starlings, juncos, turkeys, etc. and those of their type correspond to long-day plants, though there does not seem to be a critical day-length for them as for plants. Their previous sexual and light histories evidently determine for the time the critical length of day. Relative direction of change of day-length seems to be the determining factor. Guinea pigs, Guinea fowl, ground squirrels and sticklebacks correspond to everblooming plants.

Even the women of Patagonia and the Eskimo fail to have sexual or menstrual cycles in the long arctic night and the men lose all sexual activity and libido also, to recover and resume sexual cycles when the daylight reappears in spring. Dr. F. Cook, who reported this from observations with the Peary Expedition in 1894, pointed out that the men of the Peary Party were affected similarly by the conditions (96).

#### CONCLUSION

It is already evident that there are numerous variations as among the different species in each class in relation to periodicity of sexual cycles associated with changes in length of day. In addition, many other factors, such as changes of temperature, food, humidity, and rainfall, play varying rôles (61, 101).

If we ask what has led to the differentiation of some species to respond to lengthening days, of others to shortening days, and of still others to be indifferent to length of day or to respond to other factors in the environment, or, perhaps, to none, we are compelled to fall back upon speculation or conjecture.

One may suggest that, in the countless generations of animals and plants living under different types of season, with different times of stress and danger to the offspring, *that* type of sexual cycle which best meets these obstacles to success and survival for each species has been evolved for it under natural selection. Those not producing their young in a favorable season died out, because their sexual cycles were not adapted to their environment. Those that most nearly conformed survived. Some species developed a relation to one factor in the environment which set off or controlled the sexual mechanism

at the right time, such as the very regular change in length of day. Sometimes they became related to it in one way like starlings and ferrets; sometimes in another, like sheep. This depended also on length of gestation period in some cases. Other animals and plants were better served by a factor like change in food (82), in temperature (79) or in humidity (61, 101), and were selected in relation to it.

We are still only in the beginnings of these studies of sexual photoperiodicity

or photoperiodism and most of our conjectures must serve only as working hypotheses, to be tested out on each species in turn, in the hope that some great or broad correlating principle may emerge as the smoke of controversy and conflicting opinions clears with the increase of more definite knowledge. We must not deceive ourselves by thinking we have the keys to the whole of the problems as yet. They are still beyond our grasp, but coming nearer.

## LIST OF LITERATURE

## Plants

- (1) ADAMS, J. 1920. *Bot. Gaz.*, 60: 153-156.
- (2) ——. 1923. *Ann. Bot.*, 37: 75-94.
- (3) ——. 1925. *Am. J. Bot.*, 12: 398-412.
- (4) ALLARD, H. A. 1932. *J. Agr. Res.*, 44 (2): 127-137. *Ecol.*, 13: 221-234.
- (5) ARTHUR, J. M., and J. D. GUTHRIE. 1927. *Mam. Hort. Soc. N. Y.*, 3: 73-74.
- (6) BRECKLEY, E. E. 1931. *Ann. Mo. Bot. Gard.*, 18: 573-601.
- (7) CURTIS, G. 1890. *Rev. Gén. d. Bot.*, tom II. cited from ADAMS. 1923.
- (8) EATON, F. M. 1924. *Bot. Gaz.*, 77: 311-321.
- (9) ENOMOTO, N. 1929. *Proc. Crop. Sci. Japan*, 3: 32-37, cited from *Biol. Abstr.*, 5(10): 2245. #22941.
- (10) FLAMMARION, C. 1898(?). *Exp. Sin. Res.*, 10(2): 103-114.
- (11) FLINT, L. H. 1934. *Science*, 80(2063): 38-40.
- (12) GARNER, W. W. 1929. *Proc. Intern. Congr. Plant. Sci.*, 1926, 2: 1050-1055.
- (13) GARNER, W. W., and H. A. ALLARD. 1920. *J. Agr. Res.*, 18: 553-606.
- (14) ——. 1922. *Science*, 55: 582-583.
- (15) ——. 1923. *J. Agr. Res.*, 23: 871-919.
- (16) ——. 1925. *Ibid.*, 31: 555-556.
- (17) ——. 1927. *Science*, 66: 40-42.
- (18) ——. 1930. *J. Agr. Res.*, 41: 719-735.
- (19) ——. 1931. *Ibid.*, 42: 439-444 and 629-651.
- (20) GARNER, W. W., C. W. BACON and H. A. ALLARD. 1924. *Ibid.*, 27: 119-156.
- (21) GARNER, W. W. 1933. *Plant Physiol.*, 8(3): 347-356.
- (22) GILBERT, B. E. 1926. *Bot. Gaz.*, 81: 1-24.
- (23) KELLERMAN, K. F. 1926. *QUART. REV. BIOL.*, 1: 87-94.
- (24) KLEBS, G. 1918. *Flora*, N. F. 11/12(111/112): 128-151. *Festschr. Stahl.*
- (25) LOREWING, W. F. 1933. *Proc. Soc. Exp. Bio. Med.*, 30(9): 1215-1220.
- (26) MANOLOV, E. O. 1929. *Am. J. Phys. Anthropol.*, 13(1): 29-68.
- (27) NIGHTINGALE, G. T. 1927. *Univ. Wisconsin, Agr. Exp. Sta. Res. Bull.*, 74: 1-68.
- (28) NOGUTI, Y. 1927. *J. Sci. Agr. Soc. Japan*, 199: 487-500.
- (29) PHILIP, G. 1932. *Nature*, 130(3287): 665.
- (30) PLITT, T. M. 1932. *Plant Physiol.*, 7: 337-339.
- (31) RAMSLEY, F. 1933. *Univ. Colorado Stud.*, 20(2/3): 257-263.
- (32) REDDINGTON, G. 1929a. *Biol. Rev.*, 4: 180-208; b. *Trans. Roy. Soc. Edin.*, 56: 247-272.
- (33) RICHET, F. O., and G. F. SYRAUX. 1932. *Am. Nat.*, 66: 433-443.
- (34) SCHAFFNER, J. H. 1919. *Science*, 50: 311-312.
- (35) ——. 1921. *Bot. Gaz.*, 71: 197-219.
- (36) ——. 1923. *Ecology*, 4: 323-334. *Ohio J. Sci.*, 23: 149-159.
- (37) ——. 1927. *Bot. Gaz.*, 84: 440-449.
- (38) ——. 1928. *Ibid.*, 90(3): 279-298.
- (39) ——. 1931. *Am. J. Bot.*, 18(6): 424-430.
- (40) SCHIMPER, A. F. W. 1903. *Plant Geography upon a Physiological Basis*. English Translation, Oxford.
- (41) THOMPSON, H. C. 1932. Paper read at Am. Soc. Plant Physiol., Dec. 29.
- (42) TINCNER, M. A. H. 1929. *J. Roy. Hort. Soc.*, 54(2): 354, cited from Rameley.
- (43) VÖCHTING, H. 1893. *Jahrb. f. wiss. Bot.*, 25: 149, cited from Adams, 1923.
- (44) WANN, F. B. 1925. *Am. J. Bot.*, 12: 307-318.

## Animals

- (45) ALLANSON, M. 1931. *J. Physiol.*, 71: XX.  
 (46) —. 1932. *Proc. Roy. Soc., B*, 110: 295-310.  
 (47) ALLANSON, M., I. W. ROWLANDS and A. S. PARKES. 1934. *Ibid.*, 115: 410-421.  
 (48) ALLANSON, M., and R. DRANKLEY. 1934. *Ibid.*, 116: 170-185.  
 (49) BACHMAN, C., J. B. COLLIP, H. SELYE. 1934. *Proc. Soc. Exp. Biol. Med.*, 32: 544.  
 (50) BAKER, J. R., and R. M. RANSON. 1932. *Proc. Roy. Soc., B*, 110: 313-322.  
 (51) —. 1932b. *Ibid.*, 112: 39-46.  
 (52) —. 1933. *Ibid.*, 113: 486-495.  
 (53) BENOIT, J. 1934. *Compt. Rend. Acad. Sci. Paris*, 199: 1671-1673.  
 (54) BISSONNETTE, T. H. 1930. *Am. Jour. Anat.*, 45: 299-305.  
 (55) —. 1930b. *Ibid.*, 46: 477-497.  
 (56) —. 1931a. *Jour. Exp. Zool.*, 58: 281-319.  
 (57) —. 1931b. *Physiol. Zool.*, 4(4): 542-574.  
 (58) —. 1932a. *Ibid.*, 5(1): 92-123.  
 (59) —. 1932b. *Proc. Roy. Soc., B*, 110: 322-336.  
 (60) —. 1932c. *Camb. Univ. Agric. Soc. Mag.*, 3(3): 14-18.  
 (61) —. 1932d. *Nature (London)*, 129: 612.  
 (62) —. 1932e. *Science*, 76: 253-255.  
 (63) —. 1933a. *QUART. REV. BIOL.*, 8(2): 201-208.  
 (64) —. 1933b. *Biol. Bull.*, 65(3): 452-467.  
 (65) —. 1935a. *Ibid.*, 68(2): 300-313.  
 (66) —. 1935b. *J. Hered.*, 26(7): 284-286.  
 (67) —. 1935c. *Jour. Exp. Zool.*, 71(2): 341-373.  
 (68) —. 1935d. *Anat. Rec.*, 65(2): 159-168.  
 (69) —. 1935e. *J. Exp. Biol.*, 12(4): 315-320.  
 (70) BISSONNETTE, T. H., and M. H. CHAPNICK. 1930. *Am. Jour. Anat.*, 45: 307-343.  
 (71) BISSONNETTE, T. H., and A. P. R. WADLUND. 1931. *Jour. Morph.*, 52: 403-428.  
 (72) —. 1932. *J. Exp. Biol.*, 9: 339-350.  
 (73) —. 1933. *Bird Banding*, 4: 8-18.  
 (74) BISSONNETTE, T. H., and A. J. ZUTKO. 1936. *Avuk*, 53(1): 30-50.  
 (75) COLE, L. J. 1933. *Avuk*, 50(3): 284-296.  
 (76) COLLIP, J. B., H. SELYE, D. L. THOMSON and J. B. WILLIAMSON, 1933a. *Proc. Soc. Exp. Biol. Med.*, 30(5): 590-591.  
 (77) —. 1933b. *Ibid.*, 30(5): 665-7.  
 (78) COLLIP, J. B., H. SELYE and D. L. THOMSON. 1934. *Ibid.*, 31(6): 682-3.  
 (79) CRAIG-BENNETT, A. 1931. *Phil. Trans. Roy. Soc. Lond.*, B, 219: 197-279.  
 (80) DEMMEY, E. W., H. J. MYERS, W. C. YOUNG, and D. B. JENNISON. *Am. J. Physiol.*, 109(2): 307-311.  
 (81) EYFING, G. 1924. *Avuk*, 41: 439-444.  
 (82) FRIEDMAN, M. H., and G. S. FRIEDMAN. 1934. *Proc. Soc. Exp. Biol. Med.*, 31(7): 842-3.  
 (83) HAMMOND, J., and F. H. A. MARSHALL. 1930. *Proc. Roy. Soc., B*, 105: 607-637.  
 (84) HAMMOND, J., and A. WALTON. 1934a. *J. Exp. Biol.*, 11(3): 307-319.  
 (85) —. 1934b. *Ibid.*, 11(3): 320-325.  
 (86) HANSON, N. 1930. 4th. World's Poultry Congr. paper #45. *Biol. Abstr.*, 6(3): #78943.  
 (87) HILL, M., and A. S. PARKES. 1930a. *J. Physiol.*, 69: XVIII-XIX.  
 (88) —. 1930b. *Proc. Roy. Soc., B*, 107: 39-49.  
 (89) —. 1932a. *Ibid.*, 112: 146-153.  
 (90) —. 1932b. *Ibid.*, 112: 153-158.  
 (91) —. 1933. *Ibid.*, 113: 530-536; 537-540; 542-544.  
 (92) —. 1934. *Ibid.*, 115: 14-17.  
 (93) JOHNSON, G. E., and N. J. WADE. 1931. *Biol. Bull.*, 61(1): 101-114.  
 (94) KREBLE, F. 1910. *Plant Animals, A Study in Symbiosis*. Camb. Press. Ch. VIII.  
 (95) LIPPINCOTT, W. A., and L. E. CARD. 1934. *Poultry Production*. Lea and Febiger, Philadelphia.  
 (96) LERWELLYN, LL. J. 1932. *Nature*, 129: 868.  
 (97) LEE COOK, F. 1894. *N. Y. J. Gyn. Obst.*  
 (98) MANOILOV, E. O. 1929. *Am. J. Phys. Anthropol.*, 13(1): 19-69.  
 (99) MARCOVITCH, S. 1923. *Science*, 58: 537.  
 (100) MARSHALL, F. H. A. 1904. *Quart. Jour. Micro. Sci.*, 48: 323-346.  
 (101) —. 1922. *Physiology of Reproduction*. Longmans, Green and Co., London.  
 (102) —. 1932. *Nature*, 129: 344 and 361.  
 (103) MARSHALL, F. H. A., and F. P. BOWDEN. 1934. *J. Exp. Biol.*, 11(4): 409-422.  
 (104) MARTIN, M. 1698. *Voyage to St. Kilda*. (1694) London, p. 35.  
 (105) MEYER, R. K., and E. L. GUSTUS. 1935. *Science*, 81: 208-210.  
 (106) MIYAZAKI, H. 1934. *Sci. Rep. Tohoku Imp. Univ. 4th Ser. Biol.*, 9(2/3): 193-203.  
 (107) —. 1935. *Ibid.*, 9(4): 427-429.  
 (108) MOORE, C. R., G. W. SIMMONS, L. J. WELLS, M. ZALUSKY and W. O. NELSON. 1934. *Anat. Rec.*, 60(3): 279-290.  
 (109) PARKER, G. H. 1931. *Coll. Nat. M. B. L. Woods Hole, Mass.*, 6(4): 93, 96-100.  
 (110) —. 1932. *Humoral Agents in Nervous Activity, with Special Reference to Chromatophores*. Camb. Univ. Press. 79 pp.  
 (111) ROWAN, WM. 1925. *Nature*, 115: 494-5.

- (111) ROWAN, WM. M. 1927a. *Ibid.*, 119: 351.  
 (112) —. 1927b. *Proc. Boston Soc. Nat. Hist.*, 38(6): 147-189.  
 (113) —. 1928. *Nature*, 122: 11-12.  
 (114) —. 1929. *Proc. Boston Soc. Nat. Hist.*, 39(5): 151-208.  
 (115) —. 1930. *Proc. Nat. Acad. Sci.*, 16(7): 520-525.  
 (116) —. 1931. *The Riddle of Migration*. Williams and Wilkins Co., Baltimore; Bailliere Tindall and Cox, London.  
 (117) SHELVE, H., J. B. COLLIP and D. L. THOMSON. 1934. *Proc. Soc. Exp. Biol. Med.*, 31(4): 487-8.  
 (118) SHELVE, H., C. BACHMAN, D. L. THOMSON and J. B. COLLIP. 1934. *Ibid.*, 31(9): 1113-5.  
 (119) SHAPIRO, B. G., and H. A. SHAPIRO. 1934. *J. Exp. Biol.*, 11(1): 73-80.  
 (120) SCHÄFER, E. A. 1907. *Nature*, 77: 159-163.  
 (121) SMITH, P. E., R. T. ENGLE and H. H. TYNDALE. 1934a. *Proc. Soc. Exp. Biol. Med.*, 31(6): 744.  
 (122) —. 1934b. *Ibid.*, 31(6): 745-6.  
 (123) WELLS, L. J. 1934. *Anat. Rec.*, 60(4); suppl. p. 53.  
 (124) —. 1935. *Ibid.*, 62(4): in press, Cited from Wistar Bibl. Card. (abstr.).  
 (125) WHETHAM, E. O. 1933. *J. Agr. Res.*, 23(3): 383-419.  
 (126) ZUCKERMAN, S. 1932. *The Social Life of Monkeys and Apes*. New York, Harcourt Brace and Co.  
 (127) ZWARENSTEIN, H., and SHAPIRO, H. A. 1933. *J. Exp. Biol.*, 10: 372-378.





## THE SPINAL ACCESSORY NERVE AND ITS MUSCULATURE

BY WILLIAM L. STRAUS, JR. AND A. BRAZIER HOWELL

*Department of Anatomy, Johns Hopkins University*

### INTRODUCTION

THE fact that in mammals the so-called accessory field of musculature, comprising the trapezius and sternocleidomastoid muscles, is innervated both by ramus lateralis n. accessorii and by branches of the anterior rami of the cervical nerves, is a circumstance that has never ceased to puzzle anatomists. The present writers have been interested in this problem for a number of years and have borne it constantly in mind during the course of their investigations. At present it is almost universally believed that ramus lateralis n. accessorii is of visceral derivation. Recently, however, Addens (1933) has revived the old claim (see discussions by Fürbringer, 1897, and Lubosch, 1899) that this nerve is a spinal component of somatic origin.

Addens bases his contention on three main points: (a) the presence in a few fish of a component of n. X which he interpreted as somatic and the homologue of spinal n. XI; (b) the apparent continuity of the spinal XI nucleus with that of n. XII in some forms; and (c) the assumption of some investigators that m. trapezius is of myomeric rather than branchiomic origin. Addens thus believes that the spinal accessory nerve and trapezius sheet of musculature have somatic rather than branchiomic genesis, a contention requiring the thesis that in this respect mammals are more primitive than the dogfish.

If ramus lateralis n. accessorii be merely

a modified somatic spinal component, then the dual innervation of the spinal accessory field of musculature involves no particular problem. On the other hand, if this nerve be of visceral derivation, the double innervation of its musculature is myologically unique. In such case either the muscles are of compound visceral-somatic origin, or else, primarily visceral, some of their nerve components have secondarily shifted to follow a somatic (spinal) pathway.

### FUNCTION OF THE ACCESSORY FIELD OF MUSCULATURE

The functions of the sternocleidomastoid and trapezius muscles are well known, yet it appears advisable to stress certain features in the present connection. The former division not only nods the head and rotates it, but is of use in respiration for advancing the sternum. The trapezius is, perhaps, the most frequently used muscle of the shoulder. Its anterior portion advances and adducts the scapula voluntarily, fixes the shoulder for other movements, advances it in forced respiration, particularly in quadrupeds, and, above all, constantly maintains its posture. The middle part of the trapezius adducts the scapula, usually in synergy with the rhomboid, and the lower part retards it. It thus is seen how complicated is the rôle played by these muscles. Not the least important function is that concerned with respiration, this being most marked in forms which maintain contact of the fore feet with the ground. For example,



Longet (1861) found that if quadrupeds are made to run, following bilateral section of n. XI, they rapidly become breathless because of inability to advance the thorax.

#### MOTOR NUCLEI

Before considering peripheral conditions of n. XI, it is advisable to offer a brief résumé of the essential facts regarding the motor nuclei of the striated visceral musculature, as condensed from the literature (esp. Addens, 1933; Black, 1917, 1920; Kappers, 1920).

It is logical to assume that in the earliest phylogenetic stages, in which continuity of the branchial elements was relatively complete, there was a single, continuous column of branchial motor nuclei, including the efferent neurons of nn. V, VII, IX and X. This is the condition strongly suggested in cyclostomes. In elasmobranchs, however, and uniformly in all vertebrates of more advanced organization, the nucleus of V has separated from the remainder of the column. This is not surprising, in that the trigeminal field is the first to relinquish essentially branchial function in favor of other uses. One would expect the nucleus of VII to be the next exhibiting such a tendency, and such is the case. In elasmobranchs, dipnoans, and some teleosts the nucleus of VII still is essentially continuous with the IX-X column, but in other teleosts different degrees of specialization are exhibited. Thus the facial nucleus may partially (*Tinca*) or completely (*Silurus*) split off from that of IX-X and migrate ventrally. In others (*Gadus*, *Lophius*) there may be close connection of a part of VII with IX, these two separating from X. In this event the nucleus of VII may split into two parts, one of which remains distinct (*Gadus*).

It is generally believed that in most

fish the motor cells of X lie exclusively in the vagus motor column. There is some evidence, however, suggesting that emerging X fibers do not always arise solely from the region generally regarded as visceral motor. Thus in certain teleostomes X may be reinforced internally by fibers arising from the somatic motor region of the medulla (Haller, Kingsbury, Addens).

Addens seems to base his argument for the somatic derivation of XI chiefly on the occurrence of this supposed somatic component in three genera of bony fish (*Gasterosteus*, *Spinachia*, *Ophiocephalus*), although he found that it was absent in many other forms. In these three he detected, in the region just caudal to the calamus, a bundle of fibers arising from the spinal (somatic) motor column and joining those of X internally. There is no reason, however, for assuming that this fiber bundle represents a somatic component, much less that it is the homologue of a spinal XI, as Addens does. The bony fish are very highly specialized in a number of features, and at the present time it seems more logical to consider this fiber bundle as an actual component of X, whose cell-bodies, for some reason, have split from the main nucleus and migrated ventrally, just as have the neurons that form the nucleus ambiguus of amniotes (vide infra). Indeed, Haller (1897), who found similar fibers in *Salmo*, considered their cell-bodies as an actual part of the X complex (his ventral X nucleus). Kingsbury (1897), furthermore, also encountered "ventral horn" fibers reinforcing X in *Amia*, but he appeared to have been uncertain whether they actually belonged to cells lying in the somatic motor region. This point cannot be settled without experimental or embryological investigation. It is to be noted that Addens places much reliance upon a distinction between

visceral and somatic (spinal) regions of the medulla in his interpretation of the vagus bundle under discussion (pp. 338-340), while at the same time (p. 347) he attacks the distinction between somatic and visceral nerves as being "too schematic and open to criticism."

In some amphibians (*Trison*) the primitive arrangement of a continuous VII-IX-X column still persists, while in *Rana*, possibly reflecting the higher specialization of the Salientia, the nuclei of both VII and IX are completely separable from that of X.

In reptiles the nucleus of IX has migrated ventral to the X column and in this class, and in birds, remains distinct. In turtles for the first time there is initiated a ventral X nucleus in that there is a ventral bulge of a part of the original, dorsal X column. This becomes separated in some reptiles, such as the Crocodilia and *Varanus*. It constitutes a nucleus ambiguus of sorts, but according to Kappers (1920) this structure in reptiles represents only the posterior third of the nucleus ambiguus of mammals. This is not the locus of origin of spinal XI, as will be discussed later. It should be mentioned that in birds, according to Addens, the ventral nucleus of X (nucleus ambiguus) is of dual origin, for its caudal portion includes somatic motor elements derived ontogenetically from the nucleus of XII. This appears to be a specialization peculiar to birds.

In mammals a definite nucleus ambiguus always can be identified. In *Ornithorhynchus* it is poorly developed, being a small structure that can be clearly recognized only at the caudal limit of the nucleus vagus (Hines, 1929). It thus is more representative of conditions in reptiles than in therian mammals. On the other hand, according to Kappers, the second member of the Monotremata,

*Echidna*, has a well developed nucleus ambiguus, composed of both IX cells and ventrally migrated X elements. Hence in this animal the nucleus ambiguus apparently is quite comparable to the structure of the same name in therian mammals. The more recent investigations of Abbie (1934), however, indicate that in *Echidna* the development of this nucleus, particularly of its caudal portion, is less extensive than in placental mammals. The somatic motor element of X, described for *Echidna* by Abbie, which arises from an imperfectly separated portion of the nucleus of XII, is suggestive of the conditions reported in birds and some teleostomes. This detail is rather surprising, but it cannot be settled except by embryological and experimental studies. Conditions in the opossum (*Didelphis virginiana*) apparently are comparable to those obtaining in *Echidna* (cf. Voris and Hoerr, 1932), except that a supposed somatic motor component of X does not occur.

In general, it may be said that both marsupials and placentals possess a distinct dorsal motor nucleus that involves only X, its myological implication being with the smooth muscles of the viscera. This, accordingly, is general visceral efferent and parasympathetic in relationship. In addition, there is a more ventral, motor, nucleus ambiguus containing neurons implicated solely with the striated, branchiomeric musculature that is supplied by IX and X. This, therefore, is special visceral efferent. In other words, the nucleus ambiguus contains the motoneurons of the striated pharyngeal and laryngeal musculature, and therefore it is not surprising that these cells should be separated from those controlling smooth muscle.

It generally has been considered that in reptiles, as in Anamnia, the nucleus of origin of the spinal XI component is

located in the caudal end of the dorsal X column. Beccari, however, has claimed that in *Lacerta* at least it originates from ventral horn cells, and Addens that in crocodiles (and birds) the nucleus of XI occurs as a distinct caudal continuation of that of XII; hence these investigators believed these cells to have been derived from somatic efferent elements. If the cells in question actually belong to XI—a hypothesis which is far from proven, however—the mere fact of their being situated at this level is no proof of their derivation from the somatic motor column, for they doubtless have experienced stimuli similar to those influential in the descent of the cells that constitute the nucleus ambiguus. It is significant, moreover, that the investigations of both Kappers (1912, 1920) and Black (1920) in no wise support the above hypothesis of Beccari and Addens. Neither of the former authors speaks of a separate XI nucleus, but rather, in all investigated reptiles with limbs, they found a definite prolongation of the dorsal X column into the cervical region (*Damonina*, *Chelone*, *Alligator*, *Varanus*). In the apodial Serpentes (as *Boa*), in which a spinal accessory nerve is absent, such a cervical extension also is lacking, and the dorsal nucleus of X accordingly terminates abruptly in the lower medulla.

Kappers (1920), indeed, went so far as to state that there are a number of reasons for regarding the above cervical extension of the dorsal X column of reptiles as a true accessory nucleus. Furthermore, he found the relations of these cells to be extremely similar to those of the spinal XI nucleus in embryo sheep.

In addition, Lubosch (1899) stated that the spinal vagus (or XI) nucleus in Sauropsida occupies the dorsolateral part of the ventral horn, distinct from the more medial cell column homologous with

the nucleus of XII, this being in contrast to the claims of Addens.

A point about which there has been much controversy is that respecting the location of the motor cells that contribute to the accessory nerve of mammals. Opinions may be divided into three schools of thought. One (a) considers that the so-called bulbar part of XI arises from both the nucleus ambiguus and the dorsal nucleus of X (as Ranson, Addens). A second thesis (b) is that bulbar XI arises exclusively from the dorsal nucleus of X and thus should be considered as but a part of the vagus proper (Black, 1914; Kappers, 1920). A third (c) denies any relationship of XI with X, in man at least, but claims that bulbar XI arises from cells in direct continuity with those of spinal XI, and therefore that bulbar XI (ramus internus) and spinal XI (ramus externus) are parts of the same nerve (Darkschewitsch, Grabower).

It seems unnecessary here to review in detail all the evidence applicable to the above points, and the matter, furthermore, cannot be settled at the present stage of our knowledge. It now appears likely, however, that Lubosch, Black, Chase and Ranson, Kappers and Addens are correct in claiming that bulbar XI is actually an intrinsic part of X, and thus that the accessory nerve (XI) comprises the spinal component only. This, however, does not mean that spinal XI is unrelated to the vagus complex, but rather that it represents a later phylogenetic development that has secondarily become more or less independent of the cranial branchial cells.

Regarding the cells of spinal XI, it is generally agreed that they are located somewhere in the lateral part of the ventral horn of the spinal cord (Black, Clarke, Darkschewitsch, Dees, Van Gehuchten, Kappers, Kölliker, Lubosch, Ranson,

Roller, Vermeulen, Waldeyer), and that they constitute a more or less distinct nucleus. Addens (1933), however, has claimed that the nucleus of spinal XI "is but imperfectly separated from the rest of the cervical motor column" in most mammals. According to Bruce (1901), the nucleus of spinal XI in man gradually changes from a ventromedial location in the upper cervical region to a more dorso-lateral situation in the middle cervical segments.

In connection with the above point, we cut aseptically, under ether anaesthesia, branches of the spinal accessory nerve innervating m. trapezius of a cat. After 16 days the animal was killed, verification of the operative procedure determined by autopsy, and the cervical part of the cord fixed by injection with 95 per cent alcohol. It was embedded in paraffin, sectioned at 10 micra, and stained with gallocyenin in accordance with the method of Einarson (1932). Cells showing undoubted degenerative changes were found in the dorsolateral part of the ventral horn in a locus that is practically a direct cranial projection of the intermediolateral column of the thoracic region. Thus, in this animal at least, the nucleus of spinal XI in the middle cervical region occupies that portion of the gray matter that commonly is regarded as visceral efferent. It might further be mentioned that these affected cells were smaller than the ordinary cells of the ventral horn, a circumstance that also attests, although not conclusively, to their visceral character.

Kappers (1920) has considered the nucleus of spinal XI as being derived directly from a part of the dorsal X column, by caudo-ventro-lateral migration, and not as a caudal prolongation of the nucleus ambiguus. The close association of the nucleus spinalis XI and the nucleus ambiguus, which occurs in some

mammals, he regarded as a secondary, and not a primary development. In support of this contention he cited his studies of sheep embryos and those of Vermeulen (1918). The latter found in a number of ungulates and a cetacean (*Phocaena*) that the nucleus spinalis XI was connected with the dorsal nucleus of X. Like Kappers, Vermeulen regarded these observations as indicative of the vagal origin of spinal XI. Addens, however, discarded Vermeulen's findings as a misinterpretation—an action which we regard as unjustifiable. The proximity of the more cranial part of the spinal XI nucleus to the ventromedial ventral horn cells, as described by Bruce, might well be explained by its ventral migration to form a secondary alignment with the previously descended nucleus ambiguus in accordance with neurobiotactic principles.

We consider that not a great deal can be told from the precise position of emergence of the rootlets of spinal XI, although Lubosch (1899) laid great emphasis on this point. It does seem to us, however, that their general situation between the dorsal and ventral cervical roots, both internally and externally, is strongly suggestive of a non-somatic origin.

In summary, it now appears likely that the nucleus of spinal XI has been formed by the caudal migration of original visceral (X) components, although the probability that these have been supplemented by local accretions of additional visceral elements in the cord cannot be denied. The point to be emphasized is that the nucleus of XI appears to be entirely of visceral derivation.

#### SENSORY NUCLEI

The only sensory nuclei that concern us here are those related to the tractus solitarius. The early homologue of the nucleus of the tractus solitarius probably

consists of the nucleus lobi vagi of cyclostomes. A predominatingly descending character of the IX-X part of this tract is encountered for the first time in amphibians, this evidently being due not to any neurobiotactic influence of the gustatory centers, but probably to visceral correlation of tongue and respiratory innervation (Kappers, 1914). In all vertebrates the nucleus of the tractus solitarius appears to be the chief—if not the sole—center for reception of the visceral afferent impulses carried by nn. VII, IX, and X. In mammals at least the nuclei related to the sensory fibers of the lower branchial nerves have experienced complication. Thus, in addition to the nucleus of the tractus solitarius itself, fibers of IX and X end in relation to other cell-groups, comprising the nucleus parasolitarius, the nucleus intercalatus, and the dorsal sensory nucleus of X. The internal relationship of the sensory components of the lower branchial nerves, therefore, is much more complex than in lower vertebrates. Much experimental work remains to be done before the exact nature of the fibers ending in these several nuclei is definitely known. At any rate, the significant fact in the present discussion is that if the spinal accessory nerve be of visceral derivation, any afferent fibers which it carries might be expected to enter the tractus solitarius, if not to terminate directly in the nucleus of this tract.

In this connection the observations of Windle (1931a) on the neurofibrillar development of the spinal cord in the cat appear to be of great significance. He found that in his smallest embryos (10 mm.), fibers forming a part of spinal XI roots could be traced into the tractus solitarius in the medulla. These were more conspicuous in large embryos, in which they were supplemented by dorsal

root fibers also traceable to the tractus solitarius. That both sets of fibers probably are afferents (possibly proprioceptive) from mm. trapezius and sternocleidomastoideus is strongly suggested by the investigations of Windle (1931b) on rhesus monkeys and cats, and by those of Ranson, Davenport and Doles (1932) on cats. These indicate the likelihood that afferents from the two muscles mentioned can enter the cord (1) in direct association with the emerging motor fibers of spinal XI, or (2) directly with the cervical nerve branches to the two muscles, or (3) through the upper dorsal cervical roots by means of anastomosis with XI.

Hinsey and Corbin (1934) found evidence indicating that at least proprioceptive fibers did not follow route 3 in any of the 16 cats which they studied, but of course it is possible that they may do so in those forms in which XI-cervical anastomoses are known to occur not infrequently (*vide infra*).

Available data thus clearly indicate that afferents from the trapezius sheet reach the tractus solitarius, a circumstance strongly supportive of the thesis that spinal XI and its musculature are of visceral origin. It also appears beyond question that afferent fibers shift from an accessory to a spinal pathway during phylogeny. If spinal XI is of somatic origin it is difficult to understand why the afferent fibers would first have changed to a visceral (X) pathway, only later to shift to spinal nerves.

#### GANGLIA

In the present investigation the question of the ganglia of the nerves concerned is of considerable importance. These ganglia are of two kinds, comprising the so-called root ganglia (somatic sensory) and the trunk ganglia (visceral sensory).

Basically, nn. VII, IX and X have both

types of ganglia. In amphibians they are present, but in living reptiles, with specialized, relatively insensitive integument, the somatic sensory elements of these nerves have been lost. In mammals there are somatic sensory fibers coming from the region of the outer ear, with their cells located in the geniculate ganglion of VII (much reduced but believed still to be represented in at least some mammals), ganglion superius of IX (not always separable from g. petrosum), and ganglion jugulare of X. The trunk ganglia contain the visceral sensory neurons, and when separable they occur in a more peripheral situation than the root ganglia. These cells are located in ganglion geniculi of VII, ganglion petrosum of IX (sometimes absent in reptiles), and ganglion nodosum of X (always present, Willard, 1915).

The basic distinctiveness of these several ganglia is not conclusively established. Streeter (1905) has shown that in an early embryonic stage they are diffuse and either poorly separated or confluent. At least there appears to be no necessity for the supposition that somatic sensory neurons must separate from visceral sensory neurons, for both occur together in spinal ganglia.

An important question that here intrudes involves the position and character of the ganglion cells of the accessory nerve. In fish and amphibians the branches to the trapezius muscle leave the vagus complex peripheral to the trunk ganglion. Hence, sensory neurons of the accessory component might be located in either root or trunk ganglion of the vagus. In reptiles the accessory branches appear regularly to leave the vagus between the root and trunk ganglia. Hence no accessory neurons can occur in the latter ganglion. In mammals, however, the spinal accessory nerve has nothing to do with either ganglion of the vagus; and therefore any

sensory neurons associated with it must have shifted from either or both of the vagus ganglia to some other position.

Embryological evidence for mammals indicates quite clearly that these accessory sensory cells at first are located at the roots of the spinal XI filaments. Dohrn (1901) and Streeter (1905) believed them to be continuous with the spinal ganglion crest, while Froriep (1901) considered the two to be distinct, but overlapping, entities. In either event they could well be either somatic sensory, or visceral sensory components which had migrated somewhat centrally, or both. In addition to the root ganglia of XI in embryos, it has been shown by Barratt (1899), Lubosch (1901), Weigner (1901), Fahmy (1927), Windle (1931b), and others that in some mammals (including man), at various stages of growth, there are small extracranial ganglia in XI, as well as scattered ganglion cells throughout the trunks of both X and XI. These cells were found to be more numerous in very young individuals than in adults (Fahmy).

In adult mammals it is the rule that the spinal accessory nerve has no ganglia of sufficient size to be grossly apparent, and the question naturally arises as to what has become of the afferent XI cells during phylogeny or ontogeny. Kazzander (1891), Beck (1895-96), Lubosch (1899), Weigner (1901) and Streeter (1905) have shown that there frequently occurs an anastomosis between the dorsal root of the first one or two spinal nerves and the adjacent part of the accessory nerve. The embryological investigations of Streeter indicate quite clearly that at least many of the original ganglion cells of XI become incorporated with dorsal root ganglia of cervical nerves. Evidently, therefore, there is a marked tendency for sensory cells of XI to shift over to the spinal nerves. That such migration usually is incomplete

is, however, evidenced by the not infrequent anastomosis of the accessory with cervical nerves, and by the presence in various mammals of scattered ganglion cells along the course of XI.

#### DERIVATION OF THE SPINAL ACCESSORY FIELD MUSCULATURE

If it could be demonstrated whether the trapezius sheet of musculature has visceral or somatic origin the fact would be of the utmost importance in the present investigation. In support of the latter thesis Addens advanced the claim of Völker (1908, not seen) that in a gull (*Larus ridibundus*) m. trapezius arises from the myotomes; and that of Favaro (1903), who stated that this also is the case in the sheep. Edgeworth (1935), however, found that in the above species of *Larus*, as well as in other birds, there is no m. cucullaris (trapezius), but that the muscle (craniocervicalis) which Völker mistook for that branchial element is derived from occipital myotomes. Hence the two muscles in question are in no wise homologous. Thus Völker's statements on this point are not pertinent to the present problem.

On the other hand Lewis (in Keibel and Mall, 1910) found in man that the trapezius first (7 mm. embryos) stands more in relation to the branchial arch series of muscles than to those of myomeric derivation. Edgeworth (1911, 1926, 1935) has also found in a variety of vertebrates that the accessory field of musculature is of branchial arch origin. In view of the extensiveness of Edgeworth's investigations great emphasis should be accorded his conclusions. The contrary and isolated claim of Favaro is in need of verification.

Further light perhaps can be thrown on this question by a consideration of the proprioceptive nerve-endings. As is well known (see Hinsey, 1934), somatic muscles

regularly (but not invariably) possess muscle spindles. On the other hand, spindles are not supposed to be characteristic of visceral musculature (Hines, 1930); yet it is evident that in particular cases the latter can possess these structures, for they have been found sparingly in the masticatory muscles of rabbit (Cipollone, 1897) and pig (Cuajunco, in Hines, 1927). Furthermore, muscle spindles seem to occur in greater numbers in muscles of the limbs than in those of trunk, head and neck (Hinsey, 1934), and it has been concluded that their presence, therefore, is correlated with the diversity of use and range of activity of the muscles concerned (Hines, 1930). The trapezius complex, in addition to possessing appendicular attachment, is one of the most frequently used muscle components of the body, and accordingly it might be expected to have spindles regardless of its derivation. Thus while the presence of spindles would not necessarily indicate its somatic origin, absence of these structures would constitute evidence in favor of visceral derivation.

Willard and Lawrence (1933) found, experimentally, muscle spindles in m. sternocleidomastoideus of the mouse. Straus, using Cuajunco's modified Bielschowsky method, failed to find typical spindles in the normal m. trapezius of a 21-day pouch-young opossum (31 mm. C. R.) and of a fetal pig (59 mm. C. R.). The evidence on this point therefore is conflicting, and further investigations are necessary.

#### THE SPINAL ACCESSORY MUSCULATURE IN FISH

In the dogfish (*Squalus*)—representing the elasmobranchs—the nerve to m. trapezius is really nothing more than the largest and most posterior of the rami branchiales n. vagi, supplying segments of the gill musculature. The tra-

pezius occurs as a single division, arising from the skin and the dorsal superficial fascia over the back musculature, and inserting not only upon the shoulder girdle, but also upon the epibranchial cartilage of the last gill arch. In the latter detail it is in perfect sequence with the mm. interarcuales laterales of the other gill arches, although the latter take origin ventral to the back musculature. The conditions suggest the likelihood that the trapezius is merely a specialized, posterior division of the interarcuals.

If the latter be so, the question of the morphology is in order. As in the case of the membranous or clavicular girdle in bony fish, the cartilaginous girdle in the dogfish acts as a posterior boundary of the gill apparatus, and it is extremely likely that a part of the branchial musculature became attached to the girdle, largely for anchorage. The gill arches of living elasmobranchs, however, are morphologically incomplete, for in embryos of at least some forms there are well marked rudiments of still other branchial arches caudal to those that persist in the adult (Daniel, 1922). It accordingly appears likely that the disappearance of these posterior branchials has caused a hiatus in an originally continuous series of interarcual muscles, and that the posterior element has persisted in the form of a trapezius division, which has become specialized for the purpose of elevating and protracting the girdle.

Innervation of the trapezius sheet in elasmobranchs regularly is stated to be solely by branches of the vagus nerve, and thus Howell has found it. Nishi (1922), however, stated that in a number of selachians—but not in *Cynias*, *Alopias* and *Chimaera*—the trapezius is innervated not only by branches of the vagus, but by spinal nerves as well. He accordingly believed the muscle to be of dual origin.

It is, of course, impossible to deny that some selachians may have taken the same sort of step as reptiles in this respect, but at least this needs careful proof. Howell found branches of spinal nerves passing to the deep surface of the trapezius in the dogfish. He stimulated electrically all such that he encountered, but without result, and concluded that they were cutaneous nerves, which pierced the trapezius on their way to the integument.

Cyclostomes lack pectoral fins and girdle; hence there is no *m. trapezius* recognizable as such. In the bony fishes, skeletal details are very different from those in elasmobranchs. Typically, in the former, the common gill opening is bordered by a circle of membranous bone, continuous above with the skull. This bony arc not only constitutes the posterior boundary of the gill apparatus, but is the clavicular girdle, so-called, with which the cartilaginous pectoral girdle has come, in higher vertebrates, to fuse. It is upon this membranous girdle that all of the extrinsic muscles, both somatic and branchial, at first insert.

In sharks the visceral muscle so attached to the girdle—the trapezius—has become a muscle for moving the girdle, and has broadened and increased in power. In bony fishes, on the other hand, no muscle can move the membranous girdle, because of its firm anchorage; hence visceral muscles that may be attached to it can move only some part of the gill apparatus, and consequently they are much weaker. In the cod (*Gadus*) Howell (1933) reported two visceral slips to the girdle, one above and one below, while in other fish there at times are additional slips. Because of the extreme specialization of teleosts it is doubtful if these visceral slips can always be homologized in diverse forms. A trapezius of sorts, with vagus innervation, has been reported for *Lophius* (Guitel),



*Menidia* (Herrick, 1899), *Esox* (Vetter) and others. The absence of a trapezius has been claimed for *Amiurus* (McMurrich), *Perca* (Vetter), and *Gadus* (Herrick, 1900).

There is no reason why a trapezius should not have been lost by any number of existing fish during evolution toward extreme specialization. That it may be lacking in some is readily conceded; but existing reports of its absence are not convincing. Thus Vetter stated that in *Perca* the trapezius is a somatic muscle innervated by spinal nerves, and Herrick (1900) that in *Gadus* the trapezius stretches from the cranium to the girdle and likewise is innervated by spinal nerves. Howell dissected these genera and found that the muscle which these two authors have called trapezius is obviously a division of the trunk musculature, but that small slips with vagus innervation extend from the gill structure to the membranous girdle in both forms. This causes one to suspect that when an author reports the absence of visceral muscles to the girdle in bony fishes he was looking for a broad muscle of conventional trapezius form, and has failed to detect smaller, deeper visceral slips.

Vetter (1878) reported that the trapezius in *Esox* is innervated by both nn. IX and X, but subsequently he stated that the nerve in question may have been a lateral line branch. Howell investigated the condition in this genus but could find only vagus innervation of the trapezius.

In conclusion it may be said that a representative of m. trapezius is believed to be uniformly present in fishes, although eventually it may prove to be absent in some few forms. It is innervated, so far as known, solely by a posterior twig of the series of vagus branches supplying the posterior part of the gill musculature.

#### THE SPINAL ACCESSORY MUSCULATURE IN AMPHIBIANS

The cranial nerves of *Amblystoma* (Herrick, 1894), and apparently other Caudata as well, are much specialized, as partly indicated by the fact that nn. IX and X constitute a single, closely-knit complex (cf. Lubosch, 1899). Their roots are in intimate relationship, and but a single, large, common ganglion is apparent. No separate n. XI is present, this being represented only by the most caudal rootlets of n. X. Likewise spinal n. I arises by several roots, but habitually lacks a dorsal root ganglion, which structure, however, has been reported as present in *Salamandra* (Von Plessen and Rabinovitch, 1891, not seen). This is not supposed to contribute to the hypobranchial (hypoglossal) innervation (by sp. n. 2, or 2 and 3).

In amphibians the accessory field is undivided, with no "sternocleidomastoid" differentiated. In most Caudata at least it is broad, and arises from the superficial fascia of the back, while in Salientia it appears to have a tendency to shift toward the head, and usually is thicker. It is especially narrow in the common toad and arises exclusively from the head, so that it more closely resembles a sternocleidomastoid than it does a trapezius. In urodeles it inserts at the anterior base of the scapula, and in clavicate anurans upon the acromial process. The innervation appears to be supplied solely by a branch of the vagus, although Norris (1913) reported in *Siren* that innervation was also by small "dorsal" branches of spinal nn. 1 and 2, other small branches of which supplied m. levator scapulae. It is not at all impossible that some few amphibians have initiated the step that has been taken by the reptiles, and that their trapezius also may receive spinal branches. On the other hand, it is not improbable

that the spinal nerves which Norris found going to the trapezius were actually cutaneous nerves which pierced the muscle. At least the circumstance of spinal innervation needs verification, and if found to be so it is extremely likely that the spinal branches concerned carry only sensory fibers (vide infra).

Miner (1925) reported that in the giant salamander (*Megalobatrachus*) the ventral part of m. levator scapulae, unlike the dorsal part, inserted by an aponeurosis, and that the innervation of the former included visceral fibers from n. vagus. Neither Humphry (1871) nor Osawa (1902) reported such an occurrence in this animal, and Howell could not find it in other salamanders, including *Cryptobranchus*. Hence it is likely either that the nerve twigs which Miner encountered did not actually innervate the muscle, or else that his was an abnormal specimen.

In summary, it may be said that in amphibians there always is an undivided muscle unit representing the accessory field, innervated by a branch of the vagus nerve. Possibly in some forms this musculature may receive spinal contributions, but the point needs verification.

#### THE SPINAL ACCESSORY MUSCULATURE IN REPTILES

In modern reptiles of lizard-like conformation the accessory field arises by aponeurosis dorsal to the girdle and from the posterior part of the cranium. It inserts upon the anterior border of the scapula above the clavicle, upon the entire length of the clavicle, and upon the interclavicle. Its history suggests that in ancient reptiles insertion was upon the length of both cleithrum and clavicle, before the former disappeared, and that it constituted *the* muscle for advancing and at the same time elevating the girdle.

Fürbringer (1900) long since demon-

strated that in recent lacertilians there are encountered all stages between an undivided condition of this muscle sheet and one in which a sternocleidomastoid moiety is completely separable. In any case, the portion representing the latter usually is considerably thicker than the remainder of the muscle.

The fact that a sternocleidomastoid does not differentiate in vertebrates below the reptiles is a rather conclusive indication that the accessory field has developed from a single, dorsal, branchiomic unit, and not from both dorsal (trapezius) and ventral (sternocleidomastoid) components, as a study of amniotes might lead one to suspect.

In living reptiles the more proximal part of X is complicated to various degrees by connection with IX, XII, and the sympathetic trunk, as discussed in the excellent paper of Willard (1915). Thus IX, X (with potential XI) and XII may form an essentially single trunk, from which a number of fine twigs diverge to the trapezius. The rootlets of X extend down into the cord, at times as far as the third cervical segment (cf. Lubosch, 1899). Occasionally it has been reported, as in *Salvator* (Fischer, 1852) and *Chelonia* (Bendz, 1843), that the most caudal vagus rootlets form a separate nerve, which undoubtedly represents a spinal XI. One can hardly doubt that any trapezius branches diverging from a cranial complex encompassing X elements are actually X (XI) components, and they have always been so reported as present except in *Chamaeleo* and *Agama* (Fischer), *Trionyx* (Ogushi), and *Anolis*. In *Anolis carolinensis*, Willard claimed that there is no cranial innervation of the trapezius. An animal of such small size is difficult to investigate grossly, and in order to determine this point we examined a large species of West Indian *Anolis* belonging to the U. S.

National Museum. In this individual X and XII anastomosed to form a stout trunk from which the trapezius sheet received innervation. It is hardly likely that this situation obtains in one species of a particular genus and not in another. In view of this, the conditions as reported in *Chamaeleo* and *Agama* by Fischer over 80 years ago need verification. Ogushi (1913) claimed that the plastro-squamosus of *Trionyx japonicus* (which he homologized with the sternocleidomastoid) is innervated solely by  $C_8$ , but it is likely that he was mistaken in interpreting this muscle as a representative of the accessory group.

In reptiles for the first time the accessory field regularly receives additional innervation by way of the spinal nerves. In both *Iguana* and *Sphenodon* at least three spinal nerves (3-5 or 4-6) are concerned. Apparently there has been but little curiosity regarding the composition of these nerve branches until the present investigation of the subject. In individuals of *Iguana*, under ether anaesthesia, Howell cut these nerves and stimulated the peripheral stumps. No action resulted, indicating that they carry no motor fibers to the accessory field of musculature. The central stumps were then stimulated. Through n. 3 there was no action, indicating that this branch carries only sensory fibers that are not stimuable under these conditions. Through the central stump of n. 4, action of the anterior (sternocleidomastoid) part of the muscle was produced, and through that of n. 5, action of the posterior trapezius. Spinal nn. 4 and 5 thus carry afferent fibers of a different type than those passing through n. 3. The former are electrically excitable under anaesthesia and elicit motor responses by way of vago-accessory branches to the muscle. In an additional, very large specimen, on the other hand, we

indubitably found motor innervation of the sternocleidomastoid through n. 3, and less certainly of the trapezius through n. 4.

We also investigated these conditions in an alligator, and by stimulating the peripheral stumps of the cervical nerves, ascertained that they carried no motor fibers to the accessory field of musculature.

In the light of these experiments it accordingly seems clear that afferent fibers, which presumably at an earlier stage followed the pathway of the vagus, in reptiles have shifted so as to take a spinal route, thus making a short cut. Doubtless there is involved in this step a variety of fasciculative or neurobiotactic principles, and there may be a tendency for afferent fibers to take a pathway to their neurons by the shortest practicable route. In addition, accessory motor fibers also have adopted this new pathway in reptiles, but less constantly, as indicated by the variability of their occurrence.

#### THE SPINAL ACCESSORY MUSCULATURE IN MAMMALS

In mammals the accessory field of musculature always is present. Except in Cetacea there uniformly is a m. trapezius, which usually is extensive and essentially continuous from the occiput to a level well caudal to the shoulder. Not infrequently this is partially separable into portions inserting upon scapular spine, acromion, and clavicle. In monotremes, however, there are two well separated portions, one chiefly from the head, the other from the dorsum of the thoracic region. A part representing a sternocleidomastoid always is present, even in Cetacea, occasionally (Monotremata) partially covered by the trapezius. There may be separate slips of origin from sternum and clavicle, and separate insertions upon mastoid and occiput, so that sternomastoid, sterno-

occipital, cleidomastoid, and cleido-occipital portions are distinguishable.

Innervation of both muscle divisions always is by both spinal accessory and cervical nerves except in certain long-necked ungulates. We have not encountered any contribution from C<sub>1</sub>, but this may well occur as an exception. Usually the spinal innervation comes from C<sub>2</sub>, C<sub>3</sub>, and C<sub>4</sub>, in part or in whole, either as branches from the single roots (as in the rule in the dog), or as branches, each of which is derived from components of adjoining roots, C<sub>2</sub>-C<sub>3</sub>, or C<sub>3</sub>-C<sub>4</sub> (as in man). In man, if the spinal innervation of the accessory field be contributed by C<sub>2</sub>-C<sub>3</sub>, the branch frequently will join the trunk of XI, while if it comes from C<sub>3</sub>-C<sub>4</sub> it usually follows a separate course. A partial exception to the above generalizations is encountered among long-necked ungulates (camel, llama, giraffe), in which the spinal branch of XI may be absent, the trapezius-sternomastoid complex then being supplied solely by cervical nerves (cf. Howell and Straus, 1934). In all other mammals the spinal XI apparently is present, and extends for various distances down the cord (cf. Lubosch, 1899).

In this connection it is important to know what the above-mentioned cervical branches carry in mammals. Are they purely sensory as sometimes in reptiles, or have motor fibers begun to follow this route, and to what extent? Several authors have endeavored to answer these questions.

Chauveau (1891) found in horses that m. sternomastoid was innervated by a nerve trunk formed by junction of XI with C<sub>2</sub>. Apparently using no anaesthesia, he demonstrated that pain fibers from this muscle were carried only by C<sub>2</sub>, a conclusion in entire agreement with the results obtained on cats by Windle and DeLozier (1932). Chauveau also found that the

spinal contribution to the sternomastoid carried no motor fibers, but apparently contained afferent fibers in addition to those concerned with pain. Thus stimulation of the central stump of the C<sub>2</sub> branch, with XI intact, produced contraction of the sternomastoid. All motor fibers to the sternomastoid in the horse accordingly are carried by XI. Chauveau's investigations did not include the trapezius. As far as the sternomastoid is concerned, however, its innervation is of a relatively primitive type, in contrast to the extreme condition occurring in long-necked artiodactyls, in which there is a tendency for not only the sensory but also the motor fibers completely to shift from XI to spinal nerves, so that the former nerve may entirely disappear.

Lesbre and Maignon (1908) repeated the experiments of Chauveau on horses, a cow, and dogs. They concluded that the motor supply of the trapezius-sternocleidomastoid complex in the two ungulates is entirely through the accessory nerve, whereas the cervical supply is purely sensory. Their statements concerning the dog are not entirely clear, but suggest to us that a cervical motor innervation may have been encountered. The observations of Todd (1912) on ungulates appear to confirm the conclusions reported above.

Sternberg (1898) found in the macaque that the cervical contribution to the sternomastoid carried no motor fibers, but that the trapezius, on the other hand, did receive efferents by this route. In contrast to this, however, both Russell (1897) and Sherrington (1898) encountered cervical motor innervation of both muscles in this animal. Sternberg repeated Russell's work and reached the conclusion that the latter's result with the sternomastoid was attributable to spread of electrical current from the cervical roots to the adja-

cent XI. From our experience with dogs we deem it likely that the discrepancy between these reports in large part may be explained by individual variability of the animals studied.

In an effort to settle some of the points at issue we undertook to investigate, under ether anaesthesia, the innervation of mm. trapezius and sternocleidomastoideus (divisible into two distinct parts) in a series of dogs that had already been used, mostly in experiments on the cerebrospinal fluid. At first we employed the Harvard induction coil as a source of faradic current, but found this so unsatisfactory that we

TABLE 1

*Results of electrical stimulation of cervical nerves supplying the accessory field of musculature in dogs*

*The first figure in each column indicates the number of animals in which muscular action was so secured, the second figure the total number of animals considered.*

	N. 3		N. 4
<i>Peripheral n. stump</i>			
Stern. cl. mast.....	12/22	3/21	0/8
Trapezius.....	5/21	6/20	3/8
<i>Central n. stump</i>			
Stern. cl. mast..	10/2	8/21	3/8
Trapezius.....	0/20	5/20	0/8

devised another apparatus that would furnish current of measured voltage with a sine wave current of 60 cycles. Thirty dogs were investigated, but seven of the experiments were discarded for reasons such as the following: in five instances the accidental sectioning of nerves, or the death of the animal before entire completion of the experiment; and in two cases the entire absence of action of the accessory field of musculature following stimulation of *either* stump of all the sectioned cervical nerves. The elimination of these last experiments may be unjustified, because the cervical nerves actually may have contained neither efferent nor elec-

trically stimuable afferent fibers for this field. We have preferred, however, as a more conservative policy, to exclude these animals from our tabulations. Thus in the 23 animals included in table 1 all showed action of the accessory field musculature following stimulation of *either* the peripheral or central stumps of at least one of the sectioned upper cervical nerves. Even in this series it has been virtually impossible to be certain that no fine nerve twigs have been broken, or that all of them have been detected. Nor could it always definitely be ascertained whether C4 did or did not reach the musculature under consideration. The discrepancy in numbers of experiments listed in table 1 (as 20, 21, or 22) is attributable to several factors. Thus in two animals C3 apparently failed to innervate either m. sternocleidomastoid or m. trapezius, while in others there were such adventitious reasons as loss of a nerve stump following slipping of a knot. For these reasons, therefore, we prefer to regard the results in these particulars as tentative rather than conclusive.

The technique employed was to expose the cervical branches which supplied the accessory field and to stimulate them with a unipolar electrode. Threads were then tied to two points on each branch and the latter sectioned between the knots. The peripheral stumps were then stimulated. If action of the accessory field could be secured at all, it followed application usually of less than one-quarter, or at most one-half volt, thus establishing the presence of motor fibers. The central stumps were then stimulated. If any action followed, a current in the neighborhood of one volt was required. Such action indicated that—as in reptiles—the nerves carried stimuable afferent fibers connected with efferents of the accessory nerve, for muscular contraction resulted

even after all other pathways to the accessory field had been interrupted.

The character of these excitable afferent fibers does not concern us here, but merely that they were afferents connected with motor fibers to the accessory field, reaching the muscles by a pathway (XI) other than by the spinal nerves. The possibility must be entertained that a few of the results obtained by stimulating central stumps may have been due to axon reflexes. We were careful, however, to destroy the infrequent proximal connections between neighboring spinal nerves, and it is unlikely that axon reflexes obscured the results in more than a very small minority of cases, if at all.

From table 1 it is apparent that the sternocleidomastoid generally receives a more cranial cervical motor innervation than does the trapezius, with diminution caudalward, and that C4 does not, in our experience, so contribute. The cervical motor fibers to the trapezius, on the other hand, may reach the muscle via any of the three nerves mentioned.

Motor fibers, determined by stimulation of the peripheral stumps, were carried to some part of the accessory field by C2 in 13 out of 21 complete experiments, but only in 3 of these animals to both mm. sternocleidomastoideus and trapezius; by C3 in 8 out of 20, but in only one instance to both muscles; and by C4 in 3 out of 8, but never to both muscles. In those dogs in which both C2 and C3 were completely investigated, at least one of these nerves carried motor fibers to one or both of the muscles under consideration in 15 out of 21 instances. In 6 out of 21 animals motor fibers were carried by both C2 and C3. Complete absence of cervical motor fibers was exhibited by 5 animals.

As with the motor innervation, stim-  
ulable afferent fibers with sternocleidomas-  
toid connection have been found most

frequently to be carried by C2, but in contrast to the efferents these not infrequently are present in C4. Stimulable afferents of the trapezius, however, were detected only in C3. In this connection it is of interest to note that these fibers are distributed to the motor mechanism of the sternocleidomastoid broadly over three cervical nerves, whereas those concerned with the trapezius in our experience are confined to a single cervical pathway, and are present less frequently. It also should be noted that stimulation of the central stumps of these cervical nerves usually resulted in marked increase of respiration.

Stimulable afferents, concerned with some part of the accessory musculature, were carried by C2 in 9 out of 20 complete experiments, but never to both muscles; by C3 in 10 out of 20, but only in 2 instances to both muscles; and by C4 in 3 out of 8, but in no instance to both muscles. In the 18 cases in which both C2 and C3 reached this field, stimulable afferent fibers concerned with either or both of the muscles in question were carried by these nerves in 13 instances; but only in 3 of them were these fibers detected in both nerves.

We investigated the same features of a chimpanzee, again using ether anaesthesia. Innervation of the accessory field was by XI and a spinal branch derived from both C3 and C4. This branch was cut. Stimulation of its peripheral stump resulted in weak though definite action of the trapezius, and the same result, though in stronger degree, followed stimulation of the central stump. This shows that in this animal spinal nerves carry motor fibers to the XI field, and also stimulable afferents to the XI motoneurons.

If any of the motoneurons of the accessory field are of somatic derivation, these, whose axons follow a spinal nerve path-

way, might be expected to be the ones. Our attempts to investigate this point by experimental procedure thus far have been entirely inconclusive.

Our experiments indicate that in reptiles both afferent and efferent fibers from the accessory field for the first time have shifted over from vagus branches representing an accessory nerve to a spinal nerve pathway. In mammals the step probably is carried farther. An apparently larger proportion of motor fibers have adopted the spinal nerve course. The pattern of distribution of these motor fibers seems still unfixed, for they exhibit much variability.

The evidence suggests that afferent fibers are less conservative in the route of their distribution than are efferent fibers, and to some extent have a tendency to adopt short cuts, when such are feasible. A new afferent pathway having become established, the corresponding efferent fibers may finally come to take the same route, following the afferents according to the principle of fasciculation, as expounded by Kappers (1932).

Because the accessory field of musculature in anamniotes is innervated solely by visceral, and in amniotes by both visceral and spinal components, it frequently is assumed that in the latter group a new myological element of myomeric (somatic) origin has been added. In view of the evidence that has been presented here, it appears that such an assumption no longer is tenable; for if our interpretation be correct, the spinal branches to the trapezius complex constitute nothing more than visceral (branchial) components that have shifted so as to follow a spinal pathway.

#### CONCLUSIONS

The spinal XI nerve is to be regarded as a derivative of the vagus complex, and hence, of visceral origin. Support of this conclusion is found in the phylogeny of its motor nucleus, which evidently has been derived from the dorsal motor nucleus of X by caudoventral migration, and in the apparent course of the afferent fibers from its musculature into the tractus solitarius, an undoubted visceral sensory pathway.

Although originally a mixed nerve, with ganglion cells primarily associated with those of X, it exhibits a strong phylogenetic inclination to lose its sensory cells, by their migration onto the dorsal roots of adjacent cervical nerves. The motor fibers appear to be somewhat more conservative, but eventually they also tend to follow this new and shorter spinal pathway, and hence, to become ensheathed with emerging cervical fibers according to the principles of fasciculation. This is carried to an extreme in long-necked ungulates, in which the spinal accessory nerve tends to disappear as a gross entity. As a result, the nerve fibers of the musculature concerned come, in amniotes, to follow two separate pathways.

The stimuli for the formation of a spinal n. XI of characteristic form are obscure. It is not improbable that these involve neurobiotactic influences, among which may be suggested the constant co-functioning of this muscular field with somatic muscles of cervical innervation, the phylogenetic descent of the shoulder, and the important rôle that the trapezius and sternocleidomastoid have come to play in respiration.

#### LIST OF LITERATURE

- ASARI, A. A. 1934. The brain-stem and cerebellum of *Echidna aculeata*. *Philos. Trans. Royal Soc. London*, ser. B, vol. 224, pp. 1-74.
- ADDENS, J. L. 1933. The motor nuclei and roots of the cranial and first spinal nerves of vertebrates. Part I. Introduction. Cyclostomes. *Zeitschr. Anat. Entwickl.*, Bd. 101, S. 307-410.
- BARRATT, J. O. W. 1899. On the anatomical struc-

- ture of the ninth, tenth, eleventh and twelfth cranial nerves. *Bris. Med. Jour.*, vol. 2, pp. 837-840.
- BROCCARI, N. 1913. Sulla spertanza delle fibre del Lenhossék al sistema del nervo accessorio e contributo alla morfologia di questo nervo. *Arch. Ital. Anat. Embriol.*, vol. 11, pp. 299-351.
- . 1914. Il IX, X, XI e XII paio di nervi cranici e i nervi cervicali negli embrioni di *Lacerta muralis*. *Arch. Ital. Anat. Embriol.*, vol. 13, pp. 1-78.
- BECK, W. 1895-96. Ueber den Austritt des N. hypoglossus und N. cervicalis primus. *Anat. Hefte*, Bd. 18, S. 249-355.
- BENDZ, H. 1843. Bidrag til den Sammenlignende Anatomie af Nervus glossopharyngeus, vagus accessorius Willisii og hyoglossus hos Reptilienne. *K. Danske Vidensk. Selsk. Naturv. Math.*, Aft. Deel 10, pp. 113-152.
- BLACK, D. 1914. On the so-called "Bulbar" portion of the accessory nerve. *Anat. Rec.*, vol. 8, pp. 110-112. (Abstract.)
- . 1917a. The motor nuclei of the cerebral nerves in phylogeny: a study of the phenomena of neurobiotaxis. Part I. Cyclostomi and Pisces. *Jour. Comp. Neurol.*, vol. 27, pp. 467-564.
- . 1917b. The motor nuclei of the cerebral nerves in phylogeny: a study of the phenomena of neurobiotaxis. Part II. Amphibia. *Jour. Comp. Neurol.*, vol. 28, pp. 379-427.
- . 1920. The motor nuclei of the cerebral nerves in phylogeny: a study of the phenomena of neurobiotaxis. Part III. Reptilia. *Jour. Comp. Neurol.*, vol. 32, pp. 61-98.
- BRUCE, A. 1901. A Topographical Atlas of the Spinal Cord. *London*, 16 pp.
- CHASE, M. R., and S. W. RANSON. 1914. The structure of the roots, trunk and branches of the vagus nerve. *Jour. Comp. Neurol.*, vol. 24, pp. 31-60.
- CHAUVEAU, A. 1891. On the sensorimotor nerve-circuit of muscles. *Brain*, vol. 14, pp. 145-178.
- CIPOLLONE, L. T. 1897. Ricerche sull'anatomia normale e patologica delle terminazione nervose nei muscoli striati. *Suppl. Ann. Med. Navale*, vol. 3, p. 282. (Not seen: cited by Hines, 1927.)
- CLARKE, J. L. 1858. Researches on the intimate structure of the brain, human and comparative. I. On the structure of the medulla oblongata. *Phil. Trans.*, pp. 231-259.
- DANIEL, F. 1912. The Elasmobranch Fishes. *Univ. Calif.*, 334 pp.
- DANKSCHWITZ, L. 1885. Ueber den Ursprung und den centralen Verlauf des Nervus accessorius Willisii. *Arch. Anat. Physiol., Anat. Abt.*, S. 361-378.
- DEBB, O. 1887. Ueber den Ursprung und den centralen Verlauf des Nervus accessorius Willisii. *Allgem. Zeitschr. Psychiat. psych. ger. Med.*, Bd. 43, S. 453-470.
- DOERN, A. 1901. Studien zur Urgeschichte des Wirbelthierkörpers. 18. Die Occipitalsomite bei verschiedenen Selachierembryonen. Thatsächliches. *Mitt. Zool. Sta. Neap.*, Bd. 15, S. 1-279.
- EDGEWORTH, F. H. 1911. On the morphology of the cranial muscles in some vertebrates. *Quart. Jour. Micros. Sci.*, vol. 56, pp. 167-316.
- . 1926. On the development of the coracobrachiales and cucullaris in *Scyllium canicula*. *Jour. Anat. Physiol.*, vol. 60, pp. 298-308.
- . 1935. The Cranial Muscles of Vertebrates. *Cambridge Press*.
- EDMARSON, L. 1932. A method for progressive selective staining of Nissl and nuclear substance in nerve cells. *Amer. Jour. Path.*, vol. 8, pp. 295-307.
- FAHRM, N. 1927. A note on the intracranial and extracranial parts of the ninth, tenth, and eleventh nerves. *Jour. Anat. Physiol.*, vol. 61, pp. 298-301.
- FAVARO, G. 1903. Ricerche intorno allo sviluppo dei muscoli dorsali, laterali e prevertebrali negli amnioti. *Arch. Ital. Anat. Embriol.*, vol. 2, pp. 518-577.
- FISCHER, J. G. 1852. Die Gehirnnerven der Saurier anatomisch untersucht. *Abhandl. Naturwiss. Verein Hamburg*, Abt. 2, S. 109-212.
- FRORDE, A. 1901. Ueber die Ganglienleisten des Kopfes und des Rumpfes und ihre Kreuzung in der Occipitalregion. *Arch. Anat. Physiol., Anat. Abt.*, S. 371-394.
- FÜHRINGER, M. 1897. Ueber die spino-occipitalen Nerven der Selachier und Holocephalen und ihre vergleichende Morphologie. *Festschr. 70. Geburt. C. Gegenbaur*, Bd. 3, S. 349-788. *Jena*.
- . 1900. Zur vergleichenden Anatomie der Brustschulterapparates und der Schulter-muskeln. Theil IV. *Jena. Zeitschr. Med.*, Bd. 34, S. 215-718.
- VAN GERRUCHTEN, A. 1906. Anatomie du Système Nerveux de l'Homme. *Louvain*, ed. 4. (pp. 538-539).
- GRABOWER. 1894. Ueber die Kerne und Wurzeln des Nervus accessorius und vagus und deren gegenseitige Beziehungen. *Arch. Laryng. Rhinol.*, Bd. 2, S. 143-152.
- GUTTEL, F. 1891. Recherches sur la ligne latérale



- de la baudroie (*Lepidus piscatorius*). *Arch. Zool. Expér.*, sér. 2, t. 9, pp. 125-190.
- HALLER, B. 1897. Der Ursprung der Vagusgruppe bei der Teleostiern. *Festschr. 70. Geburt. C. Gegenbaur*, Bd. 3, S. 45-101.
- HERRICK, C. J. 1894. The cranial nerves of *Amblystoma punctatum*. *Jour. Comp. Neurol.*, vol. 4, pp. 193-207.
- . 1899. The cranial and first spinal nerves of *Manidia*; a contribution upon the nerve components of the bony fishes. *Jour. Comp. Neurol.*, vol. 9, pp. 153-455.
- . 1900. A contribution upon the cranial nerves of the cod fish. *Jour. Comp. Neurol.*, vol. 10, pp. 265-316.
- HINES, M. 1927. Nerve and muscle. *QUART. REV. BIOL.*, vol. 2, pp. 149-180.
- . 1929. The brain of *Ornithorhynchus anatinus*. *Philos. Trans. Royal Soc. London*, vol. 217, pp. 156-287.
- . 1930. The innervation of the muscle spindle. Chapter VII, "The Vegetative Nervous System." *Baltimore*.
- HINNEY, J. C. 1934. The innervation of skeletal muscle. *Physiol. Rev.*, vol. 14, pp. 514-585.
- and K. B. CORBIN. 1934. Observations on the peripheral course of the sensory fibers in the first four cervical nerves of the cat. *Jour. Comp. Neurol.*, vol. 60, pp. 37-44.
- HOWELL, A. B. 1933. The architecture of the pectoral appendage of the codfish. *Anat. Rec.*, vol. 56, pp. 151-158.
- and W. L. STRAUSS, JR. 1934. Note on the spinal accessory nerve of long-necked ungulates. *Proc. Zool. Soc. London*, pp. 29-32.
- HUMPHREY, G. M. 1871. The muscles and nerves of *Cryptobranchus japonicus*. *Jour. Anat. Physiol.*, vol. 6, pp. 1-61.
- KAPPERS, C. U. A. 1912. Weitere Mitteilung über Neurobiotaxis. VII. Die phylogenetische Entwicklung der motorischen Wurzelkerne in Oblongata und Mittelhirn. *Folia neuro-biol.*, Bd. 6, S. 1-142.
- . 1914. Der Geschmack, peripher und central. Zugleich eine Skizze der phylogenetischen Veränderungen in den sensiblen VII, IX, and X Wurzeln. *Psychiat. Neurol. Bl.*, Bd. 18, S. 82-138.
- . 1920. Die vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen. *Haarlem*, Bd. 1.
- . 1932. Principles of development of the nervous system (Neurobiotaxis). Section II, pp. 43-89, in "Cytology and Cellular Pathology of the Nervous System" (vol. I), ed. by W. Penfield, *New York*.
- KAZZANDER, J. 1891. Ueber den Nervus accessorius Willisii und seine Beziehungen zu den oberen Cervicalnerven beim Menschen und einigen Haussäugethiern. *Arch. Anat. Physiol., Anat. Abth.*, S. 212-243.
- KEIBEL, F., and F. P. MALL. 1910. Manual of Human Embryology. *Philadelphia*, vol. 1 (p. 484).
- KINGSBURY, B. F. 1897. The structure and morphology of the oblongata in fishes. *Jour. Comp. Neurol.*, vol. 7, pp. 1-36.
- KÖLLIKER, A. 1867. Handbuch der Gewebelehre des Menschen. *Leipzig*, ed. 5.
- LESLE, F. X., and F. MAIGNON. 1908. Contribution à la physiologie du pneumogastrique et du spinal. *Ann. Soc. Agric. Sci. Indust. Lyon*, (1907), pp. 332-350.
- LONGET, F. A. 1861. *Traité de Physiologie. Paris*, t. I.
- LUBOSCH, W. 1899. Vergleichend-anatomische Untersuchungen über der Ursprung und die Phylogenese des N. accessorius Willisii. *Arch. mikr. Anat. Entwickl.*, Bd. 54, S. 514-602.
- . 1901. Drei kritische Beiträge zur vergleichenden Anatomie des N. accessorius. *Anat. Anz.*, Bd. 19, S. 461-478.
- McMURRICH, J. P. 1884. The myology of *Aminurus carus* (L.) Gill. *Proc. Canadian Inst.*, N. S., vol. 2, pp. 311-351.
- MINER, R. W. 1925. The pectoral limb of *Eryops* and other primitive tetrapods. *Bull. Amer. Mus. Nat. Hist.*, vol. 51, pp. 145-312.
- NIEBU, S. 1922. Zur Morphologie des M. trapezius. *Folia Anat. Japon.*, Bd. 1, S. 175-181.
- NORRIS, H. W. 1913. The cranial nerves of *Siren lacertina*. *Jour. Morphol.*, vol. 24, pp. 245-338.
- OGURA, K. 1913. Anatomische Studien an der japanischen dreikralligen Lippenschildkröte (*Trionyx japonicus*). II. Mitt. Muskel- und peripheres Nervensystem. *Morphol. Jahrb.*, Bd. 46, S. 299-562.
- OSAWA, G. 1902. Beiträge zur Anatomie des japanischen Riesensalamanders. *Mitt. Med. Fac. K.-Jap. Univ. Tokio*, Bd. 5, S. 221-427.
- PLESSEN, J. v., and J. RABINOVICZ. 1891. Die Kopfnerven von *Salamandra maculata* im vorher-rückten Embryonalstadium untersucht. *München*.
- RANDON, S. W. 1931. The Anatomy of the Nervous System. *Philadelphia and London*, ed. 4, 478 pp.
- , H. K. DAVENPORT, and E. A. DOLES. 1932. Intramedullary course of the dorsal root fibers of the first three cervical nerves. *Jour. Comp. Neurol.*, vol. 54, pp. 1-12.
- ROLLER, C. F. W. 1881. Der centrale Verlauf des

- Nervus accessorius Willisii. *Allg. Zeitschr. Psychiat.*, Bd. 37, S. 469-489.
- RUSSELL, J. S. R. 1897. An experimental investigation of the cervical and thoracic nerve roots in relation to the subject of wry-neck. *Brain*, vol. 20, pp. 35-55.
- SHERINGTON, C. S. 1898. II. Experiments in examination of the peripheral distribution of the fibers of the posterior roots of some spinal nerves. Part II. *Philos. Trans. Royal Soc. London*, ser. B, vol. 190, pp. 45-186.
- STERNBERG, M. 1898. Über den äusseren Ast des Nervus accessorius Willisii. *Arch. ges. Physiol.*, Bd. 71, S. 158-175.
- STREETER, G. L. 1905. The development of the cranial and spinal nerves in the occipital region of the human embryo. *Amer. Jour. Anat.*, vol. 4, pp. 83-106.
- TODD, T. W. 1912. Injuries of the nerve supply to the musculus brachio-cephalicus in ungulates. *Anat. Anz.*, Bd. 41, S. 639-643.
- VERMULEN, H. A. 1918. Die Accessoriusfrage. *Psychiat. Neurol. Bl.*, Bd. 22, S. 729-742.
- VETTER, B. 1878. Untersuchungen zur vergleichenden Anatomie der Kiemen- und Kiefermusculatur der Fische. *Jena. Zeitschr. Naturwiss.*, Bd. 12, S. 431-550.
- VÖLKER, O. 1908. "Contributions to the knowledge of the development of the occipital region in the gull" (Original in Czech. *Czech. Acad. Prague II*, vol. 17, pp. 1-47. Not seen: cited by Addens, 1933.)
- VORH, H. C., and N. L. HORRER. 1932. The hind-brain of the opossum, *Didelphis virginiana*. *Jour. Comp. Neurol.*, vol. 54, pp. 277-355.
- WALDHYER, W. 1889. Das Gorilla-Rückenmark. *Abhandl. K. Akad. Wiss. Berlin*, S. 1-147.
- WEIGNER, K. 1901. Beziehungen des Nervus accessorius zu den proximalen Spinalnerven. *Arch. anat. Inst.*, Bd. 17, S. 551-587.
- WILLARD, W. A. 1915. The cranial nerves of *Anolis carolinensis*. *Bull. Mus. Comp. Zool.*, vol. 59, pp. 15-116.
- and J. C. LAWRENCE. 1933. Some observations on the spinal accessory and cervical nerves in the innervation of the sternocleidomastoid muscle in the mouse. *Anat. Rec.*, vol. 55, p. 82. (Abstract.)
- WINDLE, W. F. 1931a. The neurofibrillar structure of the spinal cord of cat embryos correlated with the appearance of early somatic movements. *Jour. Comp. Neurol.*, vol. 53, pp. 71-113.
- . 1931b. The sensory component of the spinal accessory nerve. *Jour. Comp. Neurol.*, vol. 53, pp. 115-127.
- and L. C. DELOZIER. 1932. The absence of painful sensation in the cat during stimulation of the spinal accessory nerve. *Jour. Comp. Neurol.*, vol. 54, pp. 97-101.





## THE NUTRITIONAL REQUIREMENTS OF BACTERIA

By WILLIAM BURROWS

*Department of Biostatistics and Department of Biology, School of Hygiene and Public Health, the Johns Hopkins University*

THE problem of the nature and extent to which the growth of organisms is influenced by kinds of food substances available to them is one of fundamental importance in biology. The biologist has been interested in this problem not only as it concerns the higher plants and animals, but also in connection with the growth and reproduction of unicellular microorganisms—bacteria, yeasts and protozoa. The bacteriologist has been peculiarly and particularly involved in this phase of bacterial activity since a great part of his experimental work is possible only through his ability to grow these microorganisms on the so-called artificial or laboratory media. We may recall the second of Koch's postulates, *i.e.*, the organism of suspected etiological significance must be *grown* in pure culture (author's italics). This premise has been used again and again in all kinds of bacteriological work by substituting for "etiological significance" some other appropriate phrase such as "nitrogen fixing ability."

For many years, in fact since the early fermentation experiments of Pasteur (1860), microbiologists have sporadically investigated the nutritive requirements of bacteria and other unicellular organisms. That the problem has been attacked in a more or less haphazard, trial and error way is amply evidenced by the compilation of literally thousands of formulæ for culture media (*cf.* Levine and Schoenlein, 1930). The underlying theme of a great part of these researches has been that most

bacteria and similar creatures are unable to exist on any combination of pure compounds that ingenuity can devise but must have, in greater or lesser amounts, certain preparations which presumably contain substances of an obscure nature but of great potency in their ability to stimulate growth. These hypothetical substances have been called, somewhat vaguely, growth accessory substances, vitamins, activators, biocatalyzers, bios, growth hormones and the like. Within recent years the equally vague term "essential substances" has been fashionable. The existence of these active principles has been postulated not only in connection with the growth of the unicellular microorganisms but also with that of the higher plants, insects and larvae, and higher animals. Only in this last group is there order; the individual interested in the microorganisms is subject to a chaotic deluge of observations derived from experimental work that is, in many cases, of doubtful quality (*cf.* Dart, 1934). The functions of the vitamins, hormones, certain amino acids and certain elements in the metabolism of the higher animals are relatively well known and even though in many cases the precise nature of the activity is not fully understood, the terms applied have definite meaning. Very possibly because of this, analogies have been drawn between the growth of higher animals and that of microorganisms which may or may not be warranted. The term "growth hormone" is of doubtful significance in relation to microscopic creatures; the writer, at least, is not aware

of any evidence of an endocrine system in such organisms. The human tendency to regard something that has a name as a defined entity, and a chance similarity of names as implying a relation between the hypothetical somethings is unfortunate. Lotka's (1925) quotation from H. G. Wells is particularly apropos: "... when we have a name we are predisposed—and sometimes it is a very vicious predisposition—to imagine forthwith something answering to the name. . . . If I say Wodget or Crump, you find yourself passing over the fact that these are nothings, . . . and trying to think what sort of a thing a Wodget or a Crump may be. You find yourself insensibly, by subtle associations of sound and ideas, giving these blank terms attributes."

The title of this paper may be interpreted in a very broad sense but the writer has chosen to take a narrow and strictly limited point of view, so far as that has been possible. We shall be concerned with bacteria for the most part and shall not refer to the great body of excellent work on other organisms except where such reference is necessary to bring out possible broad biological relationships. Again, we shall concern ourselves only with nutritional factors, *i.e.*, those *substances* which are intimately and *specifically* related to the synthesis of protoplasm; such substances may have a catalytic type of function or may serve as sources of raw material. This unsatisfactory definition obviously omits from consideration physico-chemical factors such as surface tension, temperature, hydrogen ion concentration and a host of others as well as all reference to the oxidative reactions without which synthesis could not go on. It is admittedly a highly artificial separation but one which is allowable for the purposes of the present exposition. It has been impossible to avoid stepping over

those boundaries from time to time but such excursions have been kept at a minimum.

Two further definitions are necessary before we may proceed. The first of these is that of a synthetic medium. The early concept of a synthetic medium was that it should consist of inorganic salts together with some source of energy. While such a medium still remains the only type of solution in which autotrophic bacteria will flourish, the needs of the more fastidious bacteria have enlarged and broadened this original concept. The definition proposed by Burrows (1933) is fairly satisfactory at the moment, *i.e.*, "A synthetic medium may be defined as one in which all the constituents are definite chemical compounds of known composition and structure."

The other definition is that of growth. The writer prefers to regard growth as synthesis of new protoplasm and it is in that sense that the term is used here. We are primarily interested in the conversion of the constituents of a medium into more bacterial protoplasm; it is immaterial, if cellular division is not regarded as a process apart from growth, just how many and in what size packages this new protoplasm is wrapped. (At this point we come perilously close to the boundaries of our subject for surface-volume relations become of prime importance with increasing size of protoplasmic packages.) With this concept of growth, the enumeration of bacteria by plate counts or even by total microscopic counts becomes inadequate and Mueller's (1935a) method of nitrogen analyses or a similar means of estimation becomes obligatory.

We may, perhaps, diverge for a moment into a consideration of the implications of the term growth in relation to bacteria. The process, regarded as essentially proto-

plasmic synthesis, may be considered to have its beginnings in the specific catalytic mechanisms of the syntheses which result in that mixture, protoplasm. It is quite evident, particularly in the case of the bacteria, that the biological individuality of an organism is the result of the *specific* nature of such catalysis. (It may be noted here that the term catalyst is used in a very broad sense—catalytic activity may be due to "soluble" enzymes or to certain electro-chemical configurations at intra-cellular interfaces or whatnot.) This is obvious when one recalls that the identification of a bacterium is based on its biochemical activity, *i.e.*, its fermentations etc. and on serological reactions. The latter means of differentiation arises as a result of the antigenicity of certain protoplasmic constituents, the specific synthesis of which results in the production of a given bacterial strain. These microorganisms closely approach the ideal experimental animal for the study of the mechanisms of such syntheses for, so far as we know, they are not complicated by the integrating factors which are the inseparable companions of multicellular organization and differentiation. A somewhat shorter train of guesses is involved in connecting protoplasmic synthesis and antigenic content of a bacterium than is necessary to relate the morphology of a mammal and such synthesis.

It is no doubt apparent at this point why physico-chemical factors and the purely oxidative reactions may be provisionally left out of the present discussion of nutrition. Such influences may, in a somewhat artificial but nevertheless very real sense, be regarded for the present as non-specific. This concept of non-specificity becomes somewhat clearer with a consideration of what we have called the purely oxidative reactions. The oxidation of carbohydrates, simple organic

acids, etc. is a necessary correlary to growth—a mechanism which provides energy for the use of the growing cell or, from another point of view, an oxidation coupled with the reductive processes of synthesis. The particular source of free energy is more or less immaterial as long as it remains within what one might call the realm of biological possibility. A given bacterium may oxidize glucose, formic acid, citric acid and other such compounds with equal facility or, in the absence of these, will oxidize amino acids or whatever suitable material there may be at hand. The particular substance oxidized does not, so far as is known, influence the specific nature of the new protoplasm. While some bacteria may oxidize glucose largely to butyric acid and others oxidize the same sugar to acetic acid, the process is still non-specific in that it may be used by a variety of bacteria. In other words, the particular fuel burning under the boiler does not require that the resultant energy be dissipated in the sawing of wood rather than the pumping of water.

It is probable that a variety of approaches may be made to the problems presented by this concept of growth. Burrows and Jordan (1935) (1936) (unpublished experiments) have attempted to throw some light on growth processes by a study of apparent oxidation-reduction potentials produced in cultures, with suggestive but inconclusive results. Although other modes of attack will undoubtedly present themselves, at present, study of nutritive requirements seems to offer the most encouraging outlook. The writer is not aware that the foregoing reasoning has provided the motive for the multitude of experiments on the growth requirements of bacteria. At the same time, such studies do appear to be directed, either consciously or unconsciously,

toward the ultimate elucidation of the synthetic mechanisms involved in growth.

The present paper is not intended to be a review of the voluminous literature on bacterial nutrition. The excellent reviews of Sergent (1928), Stephenson (1930), Buchanan and Fulmer (1930) and Peskett (1933) are entirely adequate. Our present knowledge of growth requirements and growth stimulation does, however, need interpretation and integration insofar as that is possible.

While at the moment it is hardly practical to attempt a segregation of "growth promoting substances" on the basis of their chemical nature, it is possible to develop a rationalization of a sort based on what is known, or what may be inferred or hypothesized, in regard to the mechanism of the effects produced. The writer ventures to suggest a tentative scheme of this nature with the hope of bringing some order into the present chaos. Four defined categories into which growth promoting activities may be distributed are proposed. These categories are:

1. *Indispensable elements*. While certain elements such as carbon, nitrogen, hydrogen, oxygen, phosphorus and many others are obviously necessary, either in combination or in the elementary form, to the growth of bacteria and other organisms, certain other elements, iron, copper, magnesium, etc. are probably necessary in traces.

2. *Growth accessory substances* or what are usually regarded as vitamin-like substances constitute a group exceedingly difficult to define. Suffice it to say that preparations presumably containing such substances are characterized by their marked activity in extremely low concentrations and by their indispensable character. The effect of these substances may be that of inducing growth which would not otherwise take place or, more often, producing a strongly

stimulative effect on the scanty growth presumably resulting from inadequate amounts of the active material.

3. *Essential substances*. This group may be defined as consisting of those substances which contain certain molecular configurations which must be supplied to the organism which lacks the necessary catalytic mechanisms for the synthesis of such structures from the raw material provided. This group is distinguished from Group 2 on a quantitative basis, *i.e.*, substances included here such as amino acids, must be supplied in considerably more than traces since a definite proportion of the new protoplasm will consist of such material. A further restriction, that the structure of an essential substance must be known, serves to distinguish this group. These distinctions may eventually prove to be artificial—with complete knowledge Group 2 should merge with Group 3—but they are convenient at the moment.

4. *Growth-stimulating substances* are those substances which are not indispensable but which, because of their unusual lability to bacterial oxidative mechanisms or because of their ready conversion to suitable oxidation-reduction systems or for other reasons, produce a strongly stimulative effect on bacterial growth.

#### INDISPENSABLE ELEMENTS

While it is obvious that many of the common elements, often in combination, are indispensable to bacterial growth, the position of other elements usually regarded as rare, biologically speaking, is uncertain. It is reasonable to assume, however, that some of these are actually integral portions of bacterial protoplasm and must, therefore, be supplied. It is extremely difficult to provide experimental demonstration of such indispensability for necessary amounts may be so small as to defy chemical analysis and purification pro-

cedures. It may be possible in some cases to use extrapolated curves as Burk and his associates have done in connection with nitrogen fixation with *Azotobacter* but this is open to some criticism. A great amount of research on the oligodynamic activity of metals has shown that, whether actually indispensable or not, many of these exert pronounced growth stimulating effects in very low concentrations. Although the literature has been reviewed by Buchanan and Fulmer (1930) it is of interest to point out a few specific instances of such an effect. Bertrand (1912) has demonstrated the importance of manganese in cultures of *Aspergillus*. In Raulin's medium prepared as free as possible from the element, mycelial growth but no spore formation took place. The presence of as small a quantity as 0.00001 per cent stimulated growth and spore formation markedly. Javillier (1913) showed that cadmium sulfate when present in quantities of one part in 10,000,000 markedly stimulated growth of the same fungus.

The stimulating action of iron salts on the growth of the tubercle bacillus has been noted by a number of workers including Frouin and Guillaumie (1924), Henley (1915) and Long and Seibert (1926). Ruhland (1922) came to the conclusion that iron is essential to the assimilation of carbon in the form of carbon dioxide by those bacteria which oxidize molecular hydrogen. Waksman (1927) points out that "the beneficial action of humus (on the fixation of nitrogen by *Azotobacter*) is frequently ascribed to its inorganic constituents, particularly aluminum and silicic acid. This is confirmed by the fact that the so-called artificial humus has no such effect, while the source of the natural humus influences the degree of its beneficial action. The claim that the action of the humus is due to its inorganic

constituents has been further substantiated by the fact that purified humates do not possess the stimulating effect." The recent work of Burk and his co-workers (Burk and Lineweaver, 1931; Burk, Lineweaver and Horner, 1932; Burk, 1934; Burk and Hoover, 1934) has provided convincing evidence of the importance of calcium, molybdenum, magnesium and iron in the utilization of combined nitrogen and in the fixation of molecular nitrogen by *Azotobacter*. These results strongly suggest an intimate relation between these metals and the catalysis of the synthesis of bacterial protoplasm from the carbon of carbon dioxide on the one hand and from molecular nitrogen on the other.

Perhaps one of the most interesting relations between an element and the growth of microorganisms is found in the importance of thallium for the growth of yeast. Gottbrecht (1880) first showed that thallium tartrate stimulated yeast fermentations and Knop (1885) later demonstrated the stimulating effect of thallium sulfate on the growth of the organisms. These observations have been verified since by a number of workers. Recently Richards (1932b) has pointed out that variation in the suitability of a synthetic medium for yeasts was in one instance due to the brand of asparagin used. The satisfactory brand proved to be contaminated with sufficient thallium for the needs of the organisms while the unsatisfactory brand did not contain this impurity. In the latter case growth was adequate when thallium was supplied. It is obvious, of course, that under these circumstances asparagin might be considered to be contaminated with a vitamin-like substance or even be essential in itself.

Mueller (1935c) has very recently shown that growth stimulating substances for the diphtheria bacillus not adsorbed on

charcoal consist of potassium and magnesium salts.

While minute traces of a variety of elements undoubtedly occur as contamination in most bacteriological media, the carefully purified material used in synthetic media may be deficient in the necessary traces of these elements. The activity of various preparations of growth promoting material may well be simply a matter of making up such deficiencies. On the other hand, even though an element is not actually indispensable it may exert a stimulating effect and thereby provide a source of growth stimulating activity. The writer suspects that the activity of many vitamin preparations may eventually be accounted for on some such basis for testing of the ash of such material has been neglected by a great many workers.

In connection with the activity of metals in bacterial growth it is appropriate to point out here that the suggestion that the growth of microorganisms, particularly yeasts, is prevented in synthetic media because of the presence of traces of toxic substances, presumably metals, was made by Chrzascz (1904) in criticism of Wildiers' (1901) work. These traces of metals are supposedly precipitated by organic matter included in non-synthetic media or by large inocula. This point has been made by other workers from time to time with regard to yeast growth although Tanner (1925) says that "in the light of recent work the metallic poison explanation seems very improbable."

Burnet's (1925) experiments with bacteria are of interest in connection with growth promoting activity and the neutralization of toxic substances. Nutrient agar plates which had been exposed to light for some time were found unfit to support the growth of staphylococci when these were inoculated in small amounts

although heavy inoculations did result in growth. The inhibiting agent in the medium was found to be hydrogen peroxide and growth promoting substances active under these conditions were found to be enzyme-like substances which neutralized the growth-inhibiting properties of the peroxide. Gordon and McLeod (1926) have shown that bacterial growth may be inhibited by some amino acids in relatively high concentration. Others have observed this phenomenon in a few instances. In the writer's experience cystine is markedly toxic in concentrations near saturation at neutrality and 37°C. and the presence of large amounts of tyrosine inhibits growth somewhat. Simms (1936) has recently shown that trypsin and papain exert a stimulating effect on the growth of adult chicken tissue *in vitro* due to the destruction of a growth-inhibiting substance produced by the cells themselves.

It is questionable, however, whether growth promoting activity demonstrable under the usual laboratory conditions may be considered nothing more than the neutralization of toxic substances present in the medium. Unfavorable oxidation-reduction conditions, resulting in a bacteriostatic effect such as Burnet observed, may very possibly be of considerable importance particularly in studies of growth in synthetic media. Possible pseudo-toxic effects of this type are briefly discussed under non-specific growth stimulation.

The phenomenon of toxicity is probably of some importance in mixed cultures. McLeod and Govenlock (1921) have demonstrated the production of bactericidins by certain microorganisms and Reid (1935) has recently found that a mold produces a growth-inhibiting substance active for some bacteria. Regnier and Lambin (1934) have recently demonstrated an unfavorable effect on the



growth of staphylococci in mixed culture with *B. coli*. Volterra, in his comment on this paper, interprets such results in terms of a toxic effect and derives an integral expression from which a "coefficient of toxicity" may be calculated.

#### GROWTH ACCESSORY SUBSTANCES

The search for hypothetical substances, presumably of vitamin-like nature, which exert an effect on yeast growth similar to that exerted by the vitamins on the metabolism of the higher animals, has continued somewhat irregularly since the work of Wildiers (1901). He reported, it may be recalled, that the growth of yeast in a synthetic medium was dependent on the presence of an indispensable substance of unknown nature, bios. The supposition of Williams (1919) that bios was identical with undifferentiated vitamin B stimulated an immense amount of work which has been critically reviewed by Tanner (1925) and by Buchanan and Fulmer (1930). Recently Williams *et al.* (1933) have isolated a substance which they call pantothenic acid and which they and Richards (1936) have shown to be active in the stimulation of the growth of yeast in synthetic media.

Similar studies with bacteria may be said to have begun with Grassberger (1897) who demonstrated the satellite phenomenon of bacterial colony growth. The first postulation of the importance of vitamin-like substances in bacterial growth was that of Lloyd (1916) in connection with the growth of the meningococcus. Since that time literature has accumulated which has consisted for the most part of reports of the presence of growth promoting activity in a wide variety of plant and animal tissues. The literature to 1933 has been reviewed by Peskett (1933) and it is hardly possible to add to his summary. Suffice it to say that

it has been definitely shown that suitable preparations of animal and vegetable tissues exhibit a marked stimulating activity in very low concentrations on the growth of some of the more fastidious bacteria. There has been disagreement as to the properties of such activities with the exception of solubility in water.

More recently Mueller *et al.* (1933) have shown that the diphtheria bacillus would grow in a solution of hydrolyzed casein which also contained tryptophane and Liebig's meat extract. Since the bacteria would not grow without meat extract, it presumably contained some growth factor of vitamin-like character. Mueller (1935b) has shown further that these bacteria required this factor when grown in amino acid solutions.

Knight and Fildes (1933) reported that a vitamin-containing preparation was necessary for the growth of *Cl. sporogenes* in gelatin hydrolysate solutions and Fildes and Richardson (1935) found that such vitamin material was necessary even though the basic hydrolysate medium was supplemented with certain amino acids. A study of the growth requirements of the typhoid bacillus by Fildes, Gladstone and Knight (1933) indicated that the organisms would grow in amino acid solutions but that when a purified preparation of vitamin was incorporated in the medium, several of the amino acids could be dispensed with. Although Burrows (1933) had grown *Cl. botulinum* in solutions of amino acids with no added vitamin, Fildes (1935) suggested that such positive results could be accounted for on the basis of contamination of the amino acids used with vitamin.

Allison and Hoover (1934) have found that an alcohol soluble substance from molasses and similar sources acted as a growth accessory substance in the growth of the legume nodule bacteria. In their

opinion this substance was a co-enzyme. Hughes (1932) and Knight (1935) have reported a growth factor which was necessary to the growth of certain strains of staphylococci and Sahyun *et al.* (1936) have described methods for the preparation of a growth promoting factor which not only accelerated the rate of growth of the colon bacillus but also produced an increase in maximum population.

Simms (1936) has recently shown that an "A factor" contained in blood plasma produced a reduction in the lag period and a stimulation of initial growth in adult chicken tissues growing *in vitro*. He was able to get no growth in its absence.

One of the most interesting approaches to the isolation of these active principles has been that of Koser and Saunders (1935) who have attempted to use the adsorption technique of Willstätter (1926) which has proved so fruitful in the purification of enzymes. A number of workers have noted that such growth promoting material may be adsorbed, particularly on charcoal, or, conversely, that media may be rendered unfit for supporting the growth of some bacteria by preliminary treatment with charcoal or some other adsorbing agent. Robinson and Rettger (1918) found that treatment with charcoal lowered the nutritive value of "opsine" and casein digests and Lumière (1921) showed that bios was adsorbed on Fuller's earth. The growth promoting activity for hemolytic streptococci was shown to be adsorbed on charcoal by Mueller (1922a) (1922b) and by Hosoya and Kuroya (1923) and on Fuller's earth by Funk and Friedman (1922). Miller (1924) reported that the growth stimulating properties of wort were removed by adsorption with charcoal. Factors necessary to the growth of *Streptothrix corallinus* were shown to be removed by adsorption of the medium with charcoal by Peters

*et al.* (1928) and Burrows (1932) noted that the adsorption of casein hydrolysate solutions with charcoal rendered them unfit to support the growth of *Cl. botulinum*. In contrast to this experimental evidence the report of McLeod and Wyon (1921) that the addition of charcoal to the medium exerted a stimulating effect on the growth of the Shiga dysentery bacillus is of interest although it is possible that their charcoal contained impurities which possessed growth stimulating properties.

Mueller and Kapnick (1935) have recently found that the growth promoting activity for the diphtheria bacillus present in meat extract can be adsorbed on charcoal and subsequently eluted with acid alcohol. The isolation and purification of growth promoting activity by these methods has most encouraging possibilities although in view of the observations of Mueller (1934) (1935c) that certain alcohols markedly stimulate the growth of the diphtheria bacillus, the practice of elution with alcohol and acetone and with alcohol is open to possible criticism. Such successful elution is, however, in harmony with the observations of many recent workers including Walker (1922), Knight and Fildes (1933), Allison and Hoover (1934) and Sahyun *et al.* (1936) that growth promoting activities for a variety of microorganisms are soluble in alcohol and certain immiscible solvents. Tanner (1925) points out the fairly general agreement that bios is soluble in 80 per cent alcohol.

It should be pointed out here that there are several reports of preparations indistinguishable from those containing growth accessory substances, that exert a pronounced accelerating effect on carbohydrate oxidations. The existence of such an effect apart from actual growth stimulation is a point at issue in much of

the bios literature since the activity of bios preparations has at times been based on increase in numbers of cells and at others on the intensity of fermentation. cf. Tanner (1925). More recently Tatum, Peterson and Fred (1934) have reported that preparations made from various materials produced marked effects on the butyric acid fermentation although these same workers (1935) later showed that the stimulating effect was due to asparagin. Sahyun *et al.* (1936) showed that their "activators" produced "a great acceleration of carbohydrate consumption in synthetic media." Euler and Pettersson (1921) have shown, however, that there is apparently no fixed relation between numbers of organisms and intensity of fermentation. In their experiments a 100 per cent increase in fermentation was, at times, accompanied by only a 10 per cent increase in numbers. Such data provide support for the contention made here on theoretical grounds that such oxidations are probably not specifically related to growth processes, the availability of sufficient energy being assumed. If this condition is not fulfilled, as it may not be in some synthetic media, an increased oxidation of carbohydrate or similar material will induce an increased growth as a result of a non-specific relation between the two processes.

Naumann (1919) has pointed out that the addition of a trace of peptone, 0.0005 per cent, to an inorganic salt medium markedly stimulated the multiplication of yeasts. Other workers have pointed out this same effect particularly in connection with the digestion of crystalline proteins by some of the proteolytic bacteria. While the vitamin enthusiast will quickly point out that growth promoting activity is widely distributed in nature, the very wideness of its distribution opens the way for the suspicion that very possibly such

activity is a non-specific property of a variety of organic substances rather than a property of widely distributed but *particular* substances. Hosoya and Kuroya (1923) concluded, however, that their streptococcus vitamin was different from the yeast vitamin and further that a number of amino acids tested produced no such stimulating effect. The studies of Knight (1935) appear to indicate also that some degree of specificity does exist. He has shown that a preparation active in stimulating the growth of certain pigmented races of staphylococci had no effect on the colorless varieties and that the staphylococcus vitamin was not the same as the sporogenes vitamin of Knight and Fildes (1933). The fermentation-stimulating activity of asparagin, aspartic and glutamic acids noted by Tatum, Peterson and Fred (1935) was apparently confined to the isopropyl alcohol organisms; the acetone producing bacteria were not so affected.

#### ESSENTIAL SUBSTANCES

The essential substances were defined above as those substances which contain certain molecular configurations which must be supplied to an organism which lacks the necessary catalytic mechanisms for the synthesis of such structures. Burrows (1933) has pointed out that "Any species of bacterium may, theoretically, be grown *in vitro* provided the proper conditions are fulfilled. . . . The most important single factor, in some cases, at least, is the chemical composition of the substrate. The question arises, in the case of the more fastidious bacteria: Just what constitutes the proper substrate? Nothing further should be necessary, from an empiric point of view, if sources of carbon and nitrogen are supplied in such forms that they are not toxic to the bacterial cell and yet are susceptible to

attack by the bacterial synthetic and catabolic mechanisms. Numerous failures to grow some bacteria on synthetic media constitute ample evidence that this does not always hold true. . . . These failures may be explained, in part, by the postulation of limits in the synthetic powers of the organisms in question." When the writer proposed this concept, together with experimental evidence which appeared to substantiate it, he had in mind particularly amino acids which, although they could not be synthesized by the organisms, were, nevertheless, integral portions of bacterial protoplasm.

Burrows (1932) and Mueller *et al.* (1933) showed that tryptophane was essential to the growth of *Cl. botulinum* and the diphtheria bacillus respectively. Burrows (1933) later showed that botulinus could be grown in amino acid solutions without tryptophane and withdrew his previous claim although according to Fildes (1935) tryptophane is actually essential to this organism. Fildes, Gladstone and Knight (1933) showed that *B. typhosus* required tryptophane in addition to a vitamin preparation although certain strains could be trained to grow without this amino acid. Fildes and Richardson (1935) later showed that certain amino acids were necessary to the growth of *Cl. sporogenes* and Mueller (1935b) (1935c) and Mueller and Kapnick (1935) similarly found that the diphtheria bacillus required certain amino acids together with preparations of growth promoting activity from meat extract. It seems rather definitely established that certain amino acids are actually essential to the growth of some bacteria. The findings have been somewhat diverse in that different species of bacteria appear to differ from one another in this respect. Burrows (1933) reported that cystine, leucine and proline were essential while lysine and glycine produced a strongly

stimulative effect on the growth of *Cl. botulinum* and Fildes, Gladstone and Knight (1933) found that leucine, lysine and tryptophane were essential to *B. typhosus* although leucine and lysine could be dispensed with when "sporogenes vitamin" was supplied. Mueller's (1935b) (1935c) essential amino acids included cystine, tryptophane, glutamic acid, methionine, histidine, phenylalanine, glycine and valine (he later found that phenylalanine could be dispensed with) for his HY strain and valine, leucine, methionine and glutamic acid for the Park 8 strain. Cf. Mueller and Kapnick (1935). According to Fildes (1935) *Cl. botulinum* must have cystine, tyrosine, valine and tryptophane and Fildes and Richardson (1935) reported that "tryptophane, leucine, phenylalanine, tyrosine and arginine are indispensable, while histidine, cystine, methionine and valine are highly important and possibly indispensable" to the growth of *Cl. sporogenes*. These results are summarized in the accompanying table. The amino acids which have not been shown to be essential but which exert a strongly stimulative action are enclosed in parentheses.

That bacteria do differ among themselves with regard to their growth requirements, both as to essential structures and growth accessory substances is indicative of an intimate relation between such requirements and the biological individuality of the organisms. Such physiological differences in nutrition have recently been found among species of *Euglena* by Dusi (1933). *Euglena dases* will use peptones and amino acids but not ammonium or nitrate nitrogen. *E. pisciformis* will use peptones but not amino acids or nitrogen from ammonium or nitrate salts while *E. anabaena* will grow in solutions of peptones, amino acids or ammonium salts but apparently cannot

utilize nitrate nitrogen. Three other species, *E. gracilis*, *E. stellata* and *E. klebsii* grew in the presence of any of these sources of nitrogen although growth was somewhat more rapid with the organic compounds. Carrel (1931) has pointed out that "... has led to the discovery of strains of fibroblasts, which, although morphologically identical, differ in their nutritional properties. The food requirements of a given cell type are as fundamental a characteristic as its morphologi-

importance to know whether a given growth promoting activity is specific or non-specific, for purposes of interpretation of experimental results, although such a point may seem of relatively minor significance in any particular piece of work. Such knowledge will enable us to determine whether a given activity is a general property of protoplasmic synthesis, a property of such synthesis within taxonomic groups, or, finally, whether it is concerned with the specific synthesis of

*The Amino Acid Requirements of Bacteria*

CL. BOTULINUM Burrows (1933)	CL. BOTULINUM Fildes (1935)	B. TYPHOSUS Fildes et al. (1933)	CL. SPOROGENES Fildes et al. (1935)	C. DIPHTHERIA	
				HY Mueller (1935 b)	Park 8 Mueller et al. (1935)
(Tryptophane)	tryptophane	tryptophane	tryptophane	tryptophane	.....
cystine	cystine	.....	(cystine)	cystine	.....
leucine	.....	(leucine)	leucine	.....	leucine
.....	.....	.....	(methionine)	methionine	methionine
.....	valine	.....	(valine)	valine	valine
.....	tyrosine	.....	tyrosine	.....	.....
.....	.....	.....	(histidine)	histidine	.....
(lysine)	.....	(lysine)	.....	.....	.....
(glycine)	.....	.....	.....	glycine	.....
.....	.....	.....	.....	glutamic acid	glutamic acid
proline	.....	.....	.....	.....	.....
.....	.....	.....	arginine	.....	.....
.....	.....	.....	phenylalanine	.....	.....

cal aspect. It appears that each type demands a specific diet."

#### GROWTH-STIMULATING SUBSTANCES

The inclusion of a group of "growth-stimulating substances" in the present discussion is hardly congruous with the emphasis that has been laid on specificity. While such a group is not justified on the theoretical basis adopted here, its inclusion is of considerable practical significance as will appear. It includes, as suggested above, only non-specific growth promoting activity, specific activity having a place in one of the other groups. It appears to the writer that it is of some

specific protoplasmic constituents and therefore has bearing on what has been termed here "biological individuality."

It seems probable that much of the oligodynamic activity of metals is of a non-specific nature although in some cases a strong element of specificity is involved as, for example, in the stimulating and apparently indispensable function of thallium in yeast growth. With one or two exceptions there is little or no evidence on this point at present although no doubt such evidence will be forthcoming eventually.

Although they have been included in a "specific" group, the specific activity of

some of the vitamin preparations appears doubtful at the moment, very possibly because such preparations may consist of mixtures of active principles. The sporogenes vitamin of Fildes and his co-workers will stimulate the growth not only of *Cl. sporogenes* but also that of *Cl. botulinum* and the typhoid bacillus. Knight's (1935) staphylococcus factor stimulated the growth of a number of strains of the aureus variety. Knight feels that the properties of his factor agree closely with those of Hughes' (1932) substance. The sporogenes vitamin of Knight and Fildes (1933) appears to have some properties in common with Mueller's substance. The growth promoting activity studied by Koser and Saunders (1935) and by Koser *et al.* (1935) (1936) is apparently non-specific in that it stimulated the growth of a variety of bacteria. Its relation to the growth factors studied by other workers is problematical. Simms' (1936) "A factor" has certain properties in common with the sporogenes vitamin, Knight's staphylococcus vitamin and Sahyun's "activator."

The stimulation of bacterial growth by definite chemical compounds has been studied by a number of workers. Wyon (1923) has pointed out the importance of amino acids as growth stimulants—an effect to be guarded against in experimental work involving vitamin-like activity (for example, the experience of Tatum, Peterson and Fred (1934) (1935).) Hosoya and Kishino (1925) and Quastel and Stephenson (1925) have demonstrated the importance of sulfhydryl compounds in the growth of obligate anaerobes and Gordon (1926) has pointed out the favorable influence of taurine on the growth of the gonococcus.

Hammet (1929) has demonstrated the stimulating effect of sulfhydryl compounds on cell division among certain

of the protozoa together with the interesting observation that the oxidation products of such compounds, sulfoxide, sulfonate and sulfinate retard growth. Jahn (1933) has observed this stimulating effect of sulfhydryl on the growth of *Chilomonas* which he ascribes to an effect on oxidation-reduction potential.

It seems likely that such stimulating effects are the result of the adjustment of the apparent oxidation-reduction potential of the medium from a less to a more favorable condition. The relation between such potentials and the ability of bacteria to initiate growth has recently been of considerable interest. Auel and Aubertin (1927), Dubos (1929a), Plotz and Geloso (1930) and others have established the importance of such potentials in the growth of certain obligate anaerobes and Knight and Fildes (1930) have determined a critical potential level above which *Cl. tetani* would not grow and below which growth was initiated. Similar studies of the facultative anaerobes have been made by Dubos (1929b) and of the obligate aerobes by Allyn and Baldwin (1930) (1932), Knaysi and Dutky (1934) and by Wood, Wood and Baldwin (1935). It has been shown by these workers and by Ingraham (1933) that a pseudo-toxic or bacteriostatic condition may exist in media in which the "toxicity" is the result of the poisoning action of some added compound on the potential of the medium. A variety of reducing agents will function as "growth-stimulating" substances under these conditions. Such observations are in harmony with those of Hammet with regard to the inhibiting effect of oxidized sulfur compounds and of Chambers *et al.* (1929) on the non-toxicity of dyes in the reduced form when injected into certain marine ova as contrasted with their toxicity in the oxidized state.

Burrows (1932) and Mueller (1933) found that tryptophane had a growth-stimulating effect on *Cl. botulinum* and on the diphtheria bacillus in protein hydrolysate media. Although Mueller (1935b) later showed that tryptophane was actually essential to the growth of the diphtheria bacillus, Burrows (1934) found that the function of this amino acid in the growth of botulinus was that of a non-specific growth stimulation and could be taken over by cystine. The writer has since found (unpublished experiments) that this growth-stimulating activity is also a property of suitable combinations of a sulfhydryl group with an electrically unstable carbon chain. The finding that a compound such as thiopropionamid will provide such stimulation precludes the criticism that such growth-stimulating substances may be contaminated with vitamin-like material or certain naturally occurring essential molecular structures. Mueller (1934) (1935b) has also shown that certain alcohols, notably ethyl alcohol, will, in small amounts, stimulate the growth of the diphtheria bacillus remarkably. A greatly increased growth in yeast has been obtained by many workers and most recently by Richards (1932a) when inosite was incorporated in the medium. It is difficult to understand what rôle inosite plays in the growth of yeast for apparently a great part of it is stored as such in the cells. Whether its alcoholic nature indicates anything in common with Mueller's observations is unknown.

It seems definitely established that the phenomenon of non-specific growth stimulation does exist. It is very possible that such stimulation is, in many cases, the result of marked increases in the availability of energy to the microorganisms. Sulfhydryl compounds may conceivably serve as precursors of oxidation-reduction

systems and thereby provide the mechanisms necessary to oxidation. Alcohols may serve as sources of energy in themselves while tryptophane is a possible source of pyrrole rings which may be necessary to the formation of certain oxidative catalysts. cf. Alcock's (1936) discussion.

The practical importance of the inclusion of a group of growth-stimulating substances, without regard to their possible specificity, in the tentative scheme proposed here, is apparent at this point. It is obvious that much experimental work has and will yield evidence of the existence of growth promoting activity. The thoughtless investigator will mark such activity down in the credit column of "growth hormone" or some other equally meaningless term to the inevitable confusion of his readers. If such activity may be shown to lie within or without the group of non-specific growth-stimulating substances, much will have been accomplished.

The failure of an organism to grow in a synthetic medium may be due to a variety of causes such as:

1. absence of sufficient available energy because
  - a. readily oxidizable substances are not present or
  - b. precursors of respiratory catalysts such as iron are not present in adequate amounts,
2. absence of sufficient nitrogen either
  - a. in a non-specific but available form or
  - b. in the form of essential molecular structures,
3. absence of traces of indispensable elements,
4. absence of necessary vitamin-like substances,
5. a toxic condition of the medium due either to

- a. the presence of toxic substances or
- b. an unfavorable oxidation-reduction potential.

Conversely, when growth results in a synthetic medium upon the addition of some preparation it may be the result of:

1. oligodynamic activity of metals,
2. addition of indispensable elements,
3. addition of sources of energy,
4. addition of non-specific but available nitrogen,
5. non-specific growth-stimulating activity of certain compounds,
6. addition of essential molecular structures,
7. addition of vitamin-like substances or
8. an adjustment of an unfavorable oxidation-reduction potential.

No doubt lists of such possibilities can be further extended. Lest this be regarded as carrying skepticism too far, it may be pointed out that specific examples of each of these cases can be found in the literature. It is clear from these considerations that the present tendency to group all growth promoting effects under some one head is highly undesirable. Before a new type of activity is described it should be clearly defined and experimental results should be sharply scrutinized before interpretation in terms of biocatalyzers or whatnot.

#### CARBON DIOXIDE

The significance of partial pressures of carbon dioxide in the gaseous environment of bacteria is uncertain. While the function of the gas as a respiratory stimulant in higher animals has been adequately demonstrated, its effect on single-celled microorganisms is probably somewhat more complex. Carbon dioxide has not been included in any of the four categories proposed here for the rather good reason that it does not fit. It was shown by

Wherry and Ervin (1918) that the tubercle bacillus would not grow in the complete absence of the gas. These observations were extended by a number of workers and it was found that a variety of bacteria would not grow at all or showed delayed growth when carbon dioxide was removed by absorption with alkali or washed out with CO<sub>2</sub>-free air. It has also been definitely established that partial pressures of carbon dioxide are necessary or highly advantageous when certain species of bacteria such as brucella, the gonococcus and the meningococcus are isolated from the animal host. After cultivation on laboratory media for a time these organisms are able to grow without this special atmosphere. This literature has been comprehensively reviewed by Valley (1932) and it is hardly necessary to go into it further here. Since 1932 Walker (1932), Winslow, Walker and Sutermeister (1932), Walker, Winslow, Huntington and Mooney (1934), Walker, Winslow and Mooney (1934) and Gladstone, Fildes and Richardson (1935) have attacked the problem of the function of carbon dioxide in bacterial growth particularly in liquid media. It is generally agreed that the gas is necessary to growth of cultures, presumably its presence in the proper concentration is intimately related to cell division. Walker (1932) regards the lag phase in a bacterial culture as the time necessary for such concentrations to accumulate. Notwithstanding much investigation, however, the status of the gas in relation to the growth of some bacteria is somewhat obscure. It is uncertain as to whether it does act as a stimulant to cell division as a process apart from growth or whether it is a factor in protoplasmic synthesis or possibly both. Its function as a source of carbon in the metabolism of the autotrophic bacteria was shown many years ago by Winogradsky (1890) and is



well known at present. It is quite unlikely that it fulfills such a rôle in the experiments just cited. Carbon dioxide, therefore, seems to play at least two important parts in microbial metabolism, one rather obscure, and the other relatively well understood. Other experimental work, however, appears to indicate that it may have still other and different effects. The increased titre of staphylococcal hemolysins when cultures are grown in an atmosphere containing considerable amounts of carbon dioxide as shown by Burnet, (1929) (1930), and the pronounced effect of similar atmospheres on the formation of staphylococcal food poisoning substance in Woolpert and Dack's (1933) experiments are highly suggestive. In spite of its chemical inertness, present experimental evidence seems to indicate that it occupies a unique position in relation to the metabolism of bacteria and its relegation to a niche labelled "essential" or "growth accessory" seems somewhat inadequate.

The general scheme proposed here has all the disadvantages of every attempt to impose a semi-rigid structure on biological activity. Present paucity of knowledge of the nutritional aspects of bacterial growth, however, removes the majority of such objections at the moment and at the same time such a taxonomic approach may serve the purpose of introducing a logical element into the interpretation of the present welter of experimental data. It is purely tentative in nature and will undoubtedly be subject to considerable modification with increasing knowledge. It seems probable that the group of growth accessory substances will eventually merge with that of the essential substances. Further subdivision will, however, probably be necessary. A growth promoting activity may shorten

the lag period of a bacterial culture, produce a more rapid increase in numbers, *i.e.*, shorten the generation time, or it may produce an increase in the maximum attainable population or any combination of these results. These three criteria of growth promoting activity have been used indiscriminately thus far by most workers but in the future some differentiation will have to be made and it may alter the conclusions reached here to a great extent. Such differentiation is, of course, impossible in retrospect.

While the trite remark that the line of demarcation between plants and animals runs through the bacteria has rather nebulous significance to the microbiologist, it does, nevertheless, provide a basis for the rationalization of some types of experimental work. One might venture to generalize, with an eye to the multitude of pitfalls, that the combinations of carbon, nitrogen, hydrogen, etc. satisfying the nutritional needs of plants, become more and more complex as one proceeds through the single-celled organisms to the metazoa. It is to be expected, therefore, that the type and complexity of the intramolecular configurations satisfying the growth requirements of bacteria will be extremely variable. Indeed, in view of this phylogenetic relation, if it is such, it would be surprising to find their nutritional requirements as relatively uniform as those of, for example, the mammals. That such uniformity is lacking is obvious when it is recalled that microorganisms regarded as bacteria range from the autotrophic forms to those which are designated as hemophyllic. A part of this variation is, of course, accounted for by the parasitic rôle which many bacteria assume.

On the other hand, whether the microbiologist is concerned with higher fungi,

bacteria or protozoa, it is apparent that he is dealing with protoplasm—qualitatively somewhat different perhaps, but still a substance that, regardless of its origin, has many properties in common. Certain recent work indicates that such common properties may be found in food requirements also. Tryptophane is of particular interest in this connection. The position of this substance in that group of amino acids designated as essential for the higher animals is well established. Convincing evidence of its importance in bacterial growth has been presented by a number of workers. Virtanen (1935) has recently extended the work of Kōgl *et al.* (1934) and shown that  $\beta$  indolyl acetic acid exerts a stimulating effect on the growth of peas; a type of activity which would be placed in Group 4 of the classification presented here. It is hardly necessary in this connection to recall the position of the higher animals with regard to vitamins or that of plants in relation to auxins. Still another link between the extremes of the nutritional scale is suggested by Virtanen's (1935) observation that a prolan fraction mark-

edly stimulated the development of certain seeds.

It seems, therefore, that, regarding the growth and synthetic mechanisms of bacteria, we may rest assured that the situation is quite as complex as that of the multicellular creatures and possibly more so. Bacteria may or may not be primitive but they are definitely not simple. While certain types of food requirements may be held in common, one may expect at the same time a great degree of diversity. The latter may be attributable not only to the intermediate position of these organisms in the biological world but also to their extreme lability and adaptiveness which, coupled with the parasitic relationship that exists in many cases, leads to a great variety of types of metabolic activity.

After the present MS was completed the monograph of Knight (Knight, B. C. J. G., *Bacterial Nutrition. Material for a Comparative Physiology of Bacteria*. Medical Research Council Special Report Series, No. 210, 1936) appeared. Although there are many similarities between Knight's detailed review and the condensed material presented here, the differences between the two papers appear sufficient to warrant publication of this material.

#### LIST OF LITERATURE

- ALCOCK, R. S. 1936. The synthesis of proteins *in vivo*. *Physiol. Rev.*, 16: 1-18.
- ALLISON, F. E. and HOOVER, S. R. 1934. An accessory factor for legume nodule bacteria. *J. Bact.*, 27: 561-584.
- ALLEN, W. P. and BALDWIN, I. L. 1930. The effect of the oxidation-reduction character of the medium on the growth of an aerobic form of bacteria. *J. Bact.*, 10: 417-437.
- . 1932. Oxidation-reduction potentials in relation to the growth of an aerobic form of bacteria. *J. Bact.*, 23: 369-398.
- AURIE, E. and AUBERTIN, E. 1927. Sur le potentiel d'oxydo-reduction des milieux ou croissent les anaérobies strictes et les anaérobies facultatifs. *Compt. Rend. Soc. Biol.*, 97: 1729-1730.
- BERTRAND, G. 1912. Sur le rôle capital du manganèse dans la formation des conidies de l'*Aspergillus niger*. *Compt. Rend. Acad. Sci. (Paris)* 154: 381-383.
- BUCHANAN, R. E. and FULMER, E. I. 1930. Physiology and Biochemistry of Bacteria. Williams and Wilkins, Baltimore. Vol. 2.
- BURK, D. 1934. Azotase und Nitrogenase in *Azotobacter*. *Ergebnisse der Enzymforschung*, 3: 23-56.
- and LINSEBAUER, H. 1931. The influence of calcium and strontium upon the catalysis of nitrogen fixation by *Azotobacter*. *Arch. f. Mikrobiol.*, 2: 155-186.
- and HORNBER, C. K. 1932. Iron in relation to the stimulation of growth by humic acid. *Soil Sci.*, 33: 413-451.
- and HOOVER, S. R. 1934. The preparation of humate iron and other humate metals. *Plant Physiol.*, 9: 663-669.
- BURNET, F. M. 1925. Hydrogen peroxide and

- bacterial growth. *Australian J. Exp. Biol. and Med. Sci.*, 2: 65-76.
- BURNET, F. M. 1929. The exotoxins of *Staphylococcus pyogenes aureus*. *J. Path. and Bact.*, 32: 717-734.
- . 1930. The production of staphylococcus toxin. *J. Path. and Bact.*, 33: 1-16.
- BURROWS, W. 1932. Growth of *Cl. botulinum* on casein hydrolysate and hydrolysate preparations. *J. Inf. Dis.*, 51: 298-308.
- . 1933. Growth of *Cl. botulinum* on synthetic mediums. *J. Inf. Dis.*, 52: 126-137.
- . 1934. Growth-stimulating properties of cystine and tryptophane. *J. Inf. Dis.*, 54: 164-170.
- and JORDAN, E. O. 1935. Oxidation-reduction potentials in salmonella cultures. I. The development of potential levels characteristic of species. *J. Inf. Dis.*, 56: 255-263.
- and JORDAN, E. O. 1936. Oxidation-reduction potentials in salmonella cultures. II. Characteristic potentials produced by members of the suipestifer and enteritidis groups. *J. Inf. Dis.*, 58: 259-262.
- CARREL, A. 1931. The new cytology. *Science*, New Series, 73: 298-303.
- CHAMBERS, R., POLLACK, H. and COHEN, B. 1929. Intracellular oxidation-reduction studies. II. Reduction potentials of marine ova as shown by indicators. *Brit. J. Exp. Biol.*, 6: 229-247.
- CHERZANECZ, T. 1904. Zur Kenntnis des Hefewachstums in mineralischer Nährlösung. *Cent. Bakt.*, II, *Orig.*, 13: 144-149.
- DART, E. E. 1934. Conventional bacteriologic technics in "hormone" and "vitamine" research. *Proc. Soc. Exp. Biol. and Med.*, 32: 363-365.
- DUBOS, R. 1929. The initiation of growth of certain facultative anaerobes as related to oxidation-reduction processes in the medium. *J. Exp. Med.*, 49: 559-573.
- . 1929. The relation of the bacteriostatic action of certain dyes to oxidation-reduction processes. *J. Exp. Med.*, 49: 575-592.
- DUBI, H. 1933. Recherches sur la nutrition de quelques Euglenes. II. *Ann. Inst. Pasteur*, 50: 840-890.
- BUTLER, H. VON, and PETERSON, A. 1921. Vitamin B (Biokatalysatoren) und Co-Enzyme. *Ztschr. f. physiol. Chem.*, 114: 4-16.
- FILDES, P. 1935. The tryptophane and "sporogenes vitamin" requirements of *B. botulinus*. *Brit. J. Exp. Path.*, 16: 309-314.
- , GLADSTONE, G. P. and KNIGHT, B. C. J. G. 1933. The nitrogen and vitamin requirements of *B. typhosus*. *Brit. J. Exp. Path.*, 14: 189-196.
- and RICHARDSON, G. M. 1935. Amino acids necessary for the growth of *Cl. sporogenes*. *Brit. J. Exp. Path.*, 16: 326-335.
- FROUIN, A. and GUILLAUME, M. 1924. Influence des sels de fer sur la rendement en poids du bacille tuberculeux. Action de ces sels sur l'utilisation de la glycérine. *Compt. Rend. Soc. Biol. (Paris)* 90: 831-832.
- FUNK, C. and FREDMAN, L. 1921. Vitamin requirements of certain yeasts and bacteria. *J. Biol. Chem.*, 48: 437-443.
- . 1922. Nutritional requirements in the growth of yeasts and bacteria. *J. Metabol. Res.*, 56: 851-860.
- GLADSTONE, G. P., FILDES, P. and RICHARDSON, G. M. 1935. Carbon dioxide as an essential factor in the growth of bacteria. *Brit. J. Exp. Path.*, 16: 335-348.
- GORDON, J. 1926. The value of taurine for promoting the growth of the gonococcus. *J. Path. and Bact.*, 29: 319-321.
- and McLEOD, J. W. 1926. Inhibition of bacterial growth by some amino acids and its bearing on the use of tryptic digests as culture media. *J. Path. and Bact.*, 29: 13-25.
- GOTTFRECHT, 1930. Experimentelle Untersuchungen über die Wirkungen des Thallins. Dissert. *Griefswald*, 1880, quoted by Buchanan and Fulmer.
- GRABBERGER, R. 1897. Beiträge zur Bakteriologie der Influenza. *Ztschr. f. Hyg. u. Infektionskrank.*, 25: 453-475.
- HAMMET, F. S. 1929. The chemical stimulus essential for growth by increase in number. *Protoplasma*, 7: 297-322.
- HENTLEY, R. R. 1925. The influence of iron on the growth of the tubercle bacillus upon glycerinated beef broth. *Amer. Rev. Tuberculosis*, 12: 246-259.
- HOSoya, S. and KISHINO. 1925. The influence of the sulphur-containing substances upon the growth of anaerobic bacilli. *Sci. Repts. Gov. Inst. Inf. Dis., Tokyo*, 4: 123-128.
- and KUROTA, M. 1923. Water-soluble vitamin and bacterial growth. Second Report, with special reference to chemical and physical properties of vitamin essential for the growth of hemolytic streptococci. *Sci. Repts., Gov. Inst. Inf. Dis.*, 2: 265-285.
- HUGHES, T. P. 1932. Growth requirement of staphylococcus. *J. Bact.*, 23: 437-447.
- INGRAHAM, M. A. 1933. The bacteriostatic action of gentian violet and its dependence on the oxidation-reduction potential. *J. Bact.*, 26: 573-598.
- JAHN, T. L. 1933. Studies on the oxidation-reduction potential of protozoan cultures. I. The

- effect of  $-SH$  on *Chilomonas paramecium*. *Protoplasma*, 20: 90-104.
- JAVILLIER, M. 1913. Recherches sur la substitution au zinc de divers elements chimiques pour la culture de *Aspergillus niger*. *Ann. Inst. Pasteur*, 27: 1021-1038.
- KNAYE, G. and DUTKY, S. R. 1934. The growth of *Bacillus megatherium* in relation to the oxidation-reduction potential and the oxygen content of the medium. *J. Bact.*, 27: 109-119.
- KNIGHT, B. C. J. G. 1935. An essential growth for *Staphylococcus aureus*. *Brit. J. Exp. Path.*, 16: 315-326.
- and FIELDS, P. 1930. Oxidation-reduction studies in relation to bacterial growth. III. The positive limit of oxidation-reduction potential required for the germination of *B. subtilis* spores *in vitro*. *Biochem. J.*, 24: 1496-1502.
- . 1933. A vitamin necessary for the growth of *B. sporogenes*: Its relation to auxin and other growth factors. *Brit. J. Exp. Path.*, 14: 112-124.
- KNOB, W. 1885. Ueber die Aufnahme verschiedener Substanzen durch die Pflanze, welche nicht zu den Nährstoffen gehören. *Abstr. Bot. Centr.*, 22: 35-36 (1885) quoted by Buchanan and Fulmer.
- KÖGL, F., HAAAGEN-SMIT, A. J. and ERXLEBEN, H. 1934. Über ein neues Auxin ("Hetero-auxan") aus Harn. *Ztschr. f. physiol. Chem.*, 228: 90-103.
- KORR, S. A. and SAUNDERS, F. 1935. Studies on bacterial nutrition. I. Separation of growth factors from veal infusion. *J. Inf. Dis.*, 56: 305-326.
- , FINKLE, I. and SPOELSTRA, R. C. 1935. Sources of growth factors required by certain "fastidious" bacteria. Failure of ascorbic acid to replace growth-promoting principles. *Proc. Soc. Exp. Biol. and Med.*, 32: 1270-1271.
- . 1936. Studies on bacterial nutrition. II. The distribution of a growth stimulating factor in animal and plant tissues. *J. Inf. Dis.*, 58: 121-127.
- LEVINE, M. and SCHORNLEIN, H. W. 1930. A compilation of culture media for the cultivation of microorganisms. Williams & Wilkins, Baltimore.
- LOYD, D. J. 1916. On vitamins, amino-acids, and other chemical factors involved in the growth of the meningococcus. *J. Path. and Bact.*, 11: 113-130.
- LONG, B. R. and SHIBERT, F. B. 1926. The chemical composition of the active principle of tuberculin. I. A non-protein medium suitable for the reproduction of tuberculin in large quantity. *Amer. Rev. Tuberculosis*, 13: 393-397.
- LOTKA, A. J. 1925. Elements of Physical Biology. Williams & Wilkins, Baltimore.
- LUMIERE, A. 1921. Influence des vitamines et des auximones sur la croissance des vegetaux. *Ann. Inst. Pasteur*, 35: 102-103.
- MCLEOD, J. W. and GOVERNLOCK, P. 1921. The production of bactericidins by microorganism. *Lancet*, 200: 900-903.
- and WYON, G. A. 1921. The supposed importance of vitamins in promoting bacterial growth. *J. Path. and Bact.*, 24: 205-210.
- MILLER, W. L. 1924. Wildiers' bios. *Science*, 59: 197-199.
- MURILLER, J. H. 1922. Studies on the cultural requirements of bacteria. I. *J. Bact.*, 7: 309-324.
- . 1922. Studies on the cultural requirements of bacteria. II. *J. Bact.*, 7: 325-338.
- , KLINE, K., PORTER, E. F., and GRAYBIE, A. 1933. Studies on the cultural requirements of bacteria. III. The diphtheria bacillus. *J. Bact.*, 25: 509-519.
- . 1934. Amino acids required by the diphtheria bacillus for growth. *Proc. Soc. Exp. Biol. and Med.*, 32: 318-320.
- . 1935. Studies on the cultural requirements of bacteria. IV. Quantitative estimation of bacterial growth. *J. Bact.*, 29: 383-388.
- . 1935. Studies on the cultural requirements of bacteria. V. The diphtheria bacillus. *J. Bact.*, 29: 515-530.
- . 1935. Studies on cultural requirements of bacteria. VI. The diphtheria bacillus. *J. Bact.*, 30: 513-524.
- and KAPNICK, I. 1935. Studies on the cultural requirements of bacteria. VII. Amino acid requirements of Park-Williams No. 8 strain of diphtheria. *J. Bact.*, 30: 525-534.
- NAUMANN, H. 1919. Die Lebenstätigkeit von Sprosspilzen in mineralischen Nährlösungen. *Ztschr. tech. Biol.*, 7: 1-68.
- PASTEUR, L. 1860. Memoires sur la fermentation alcoolique. *Ann. de Chim. et Phys.*, 3rd series, 58: 323-426.
- PERKETT, G. L. 1933. Growth factors of lower organisms. *Biol. Rev.*, 8: 1-45.
- PETERS, R. A., KINNERSLEY, H. W., ORR-EWING, J. and READER, V. 1928. The relation of vitamin B, to the growth-promoting factor for a streptothrix. *Biochem. J.*, 22: 445-450.
- PLÖTZ, H. and GELOSO, J. 1930. Relations entre la croissance des microorganismes anaerobies et le potentiel du milieu de culture. *Ann. Inst. Past.*, 45: 613-640.
- QUASTEL, J. H. and STEPHENSON, M. 1925. Further observations on the anaerobic growth of bacteria. *Biochem. J.*, 19: 660-666.
- . 1925. Experiments on "strict anaerobic."

- I. Relationship of *B. sporogenes* to oxygen. *Biochem. J.*, 20: 1125-1137.
- REIGNER, J. and LAMBIN, S. 1934. Etude d'un cas d'antagonisme microbien (*B. coli*-*Staphylococcus aureus*). *Compt. Rend. Acad. des Sci.*, 199: 1682-1686.
- REID, R. D. 1935. Some properties of a bacterial inhibitory substance produced by a mold. *J. Bact.*, 29: 215-221.
- RICHARDS, O. W. 1932. The increased growth of a population of yeast obtained with inositol. *Proc. Soc., Exp. Biol. Med.*, 29: 627-629.
- . 1932. The stimulation of yeast growth by thallium, a 'bios' impurity of asparagins. *J. Biol. Chem.*, 96: 405-418.
- . 1936. The stimulation of yeast proliferation by pantothenic acid. *J. Biol. Chem.*, 113: 531-536.
- ROBERTSON, R. C. 1924. Food accessory factors (vitamins) in bacterial growth. IX. Growth of several common bacteria in a synthetic medium and relation of substances formed by them to growth of yeast. *J. Inf. Dis.*, 35: 311-314.
- ROBINSON, H. C. and RETTGER, L. F. 1918. The growth of bacteria in protein-free enzyme and acid-digestion products. *J. Bact.*, 3: 209-229.
- RUHLAND, W. 1922. Aktivierung von Wasserstoff und Kohlensäureassimilation durch Bakterien. *Ber. Deutsch. Bot. Gesell.*, 40: 180-184.
- SAHYUN, M., BEARD, P., SCHULTZ, E. W., SNOW, J. and CROSS, E. 1936. Growth-stimulating factors for microorganisms. *J. Inf. Dis.*, 58: 28-44.
- SERGEANT, A.-L. 1928. Les Facteurs de Croissance des Microbes sur Milieux Artificiels. Doin et Cie, Paris, 1928.
- SINCLAIR, H. S. 1936. The effects of physiological agents on adult tissues *in vitro*. *Science*, 83: 418-419.
- STEPHENSON, M. 1930. Bacterial Metabolism. Longmans, Green and Co., London, 1930.
- TANNER, F. W. 1925. The "bios" question. *Chem. Rev.*, 1: 397-472.
- TATUM, E. L., PETERSON, W. H. and FRED, E. B. 1934. An unknown factor stimulating the formation of butyl alcohol by certain butyric acid bacteria. *J. Bact.*, 27: 207-217.
- . 1935. Identification of asparagin as the substance stimulating the production of butyl alcohol by certain bacteria. *J. Bact.*, 29: 563-572.
- VALLBY, G. 1928. The effect of carbon dioxide on bacteria. *Quart. Rev. Biol.*, 3: 209-224.
- VIRTANEN, A. I. 1934. On the enzymes of bacteria and bacterial metabolism. *J. Bact.*, 28: 447-460.
- VIRTANEN, A. I. 1935. The chemistry of grass crops. *J. Soc. Chem. Ind.*, 54: 1015-1020.
- WAKEMAN, S. A. 1927. Principles of Soil Microbiology. Williams & Wilkins, Baltimore, 1st. Ed.
- WALKER, E. W. A. 1922. Bacterial products (accessory factors) in relation to bacterial growth. *J. Physiol.*, 56: *Proc. Physiol. Soc.*
- WALKER, H. H. 1932. Carbon dioxide as a factor effecting lag in bacterial growth. *Science*, 76: 602-604.
- , WINELOW, C.-E. A., HUNTINGTON, E., and MOONEY, M. G. 1934. The physiological youth of a bacterial culture as evidenced by cell metabolism. *J. Bact.*, 27: 303-324.
- and MOONEY, M. G. 1934. Bacterial cell metabolism under anaerobic conditions. *J. Gen. Physiol.*, 17: 349-357.
- WHERRY, W. B. and ERVIN, O. M. 1918. The necessity of carbon dioxide for the growth of *B. tuberculosis*. *J. Inf. Dis.*, 22: 194-197.
- WHITEHEAD, H. R. 1925. Studies in bacterial nutrition. III. Phosphates and the growth of streptococci. *Biochem. J.*, 20: 1147-1154.
- WILDIER, B. 1901. Une nouvelle substance indispensable au développement de la levure. *La Cellule*, 18: 313-333.
- WILLIAMS, R. J. 1919. The vitamin requirement of yeast, a simple biological test for vitamin. *J. Biol. Chem.*, 38: 465-486.
- , LYMAN, C. M., GOODYEAR, G. H., TRUBSDAIL, J. H. and HOLADAY, D. 1933. "Pantothenic acid," a growth determinant of universal biological occurrence. *J. Amer. Chem. Soc.*, 55: 2912-2927.
- WILLSTÄTTER, R. 1926. Über neue Methoden der Enzymforschung. *Naturwissenschaften*, 14: 937-941.
- WINOGRADSKY, S. 1890. Recherches sur les organismes de la nitrification. *Ann. Inst. Pasteur*, 4: 257-275.
- WINELOW, C.-E. A., WALKER, H. H., and SUTHERMISTER, M. 1932. The influence of aeration and of sodium chloride upon the growth curve of bacteria in various media. *J. Bact.*, 24: 185-208.
- WOOD, W. B., WOOD, M. L. and BALDWIN, I. L. 1935. The relation of oxidation-reduction potential to the growth of an aerobic organism. *J. Bact.*, 30: 593-602.
- WOOLFERT, O. C. and DACE, G. M. 1933. Relation of gastro-intestinal poison to other toxic substances produced by staphylococci. *J. Inf. Dis.*, 52: 6-19.
- WYON, G. A. 1923. Vitamins and bacterial growth. *J. Path. and Bact.*, 26: 441-445.



## CHARACTERS COMMON TO HIGHER PRIMATES AND CHARACTERS SPECIFIC FOR MAN (*Continued*)

By ADOLPH H. SCHULTZ

*Laboratory of Physical Anthropology, Johns Hopkins University*

DEGREES OF RESEMBLANCE BETWEEN THE  
HIGHER AND THE LOWER CATARRHINES AND  
BETWEEN MAN AND THE ANTHROPOID APES

### *Pelvis*

FEW parts of the human body have undergone more profound evolutionary changes in position, shape, and proportions than the pelvis. Chiefly due to the special mechanical requirements connected with erect posture the pelvis of man has acquired a general appearance which differs very strikingly from that of the pelves of the other higher primates. In a former paper the author (1930a) has already discussed in detail many of the differences in pelvic proportions between man and, particularly, the great apes, without, however, making more than a preliminary attempt to correlate the various dimensions of the pelvis with the general size of the animal, as represented by the height of its trunk. These correlations, possible only whenever the trunk height can be measured before the preparation of the skeleton, are most instructive in trying to interpret many of the comparative data on pelvic dimensions in primates.

According to the diagrams in Figure 10, the height of the ilium in percentage relation to the height of the ischium differs comparatively little among the primates studied, with the exception of man, who is set apart by having by far the shortest ilium in proportion to the ischium. That this exceptional position of man is not due, by chance, to an unusual

height of the human ischium, is proved by the third proportion in Figure 10 which shows the relation in size between the ischium and the trunk. In regard to this proportion man falls well within the range of variations among the other higher primates. The direct relation between the height of the ilium and that of the trunk (second proportion in Fig. 10) demonstrates conclusively that man is characterized among all the primates studied by the shortest ilium not only in relation to the ischium, but also in relation to the trunk. In all the anthropoid apes the ilium height—trunk height index is very much greater than in the macaque, langur, and man. A closely corresponding result was obtained by Waterman (1929), who studied the relation between the length of the iliac blade and the "length of the body" (from acetabulum to vertex) in some higher and lower primates. From the foregoing it is not surprising that the total height of the pelvis in percentage of the trunk height (fourth proportion in Fig. 10) is smaller in man than in any other higher primate and this, it can now be added, entirely on account of the shortness of the human ilium. The tremendous difference in relative height of the pelvis between man and, e.g., the gorilla is clearly shown by the exact drawings in the Figures 11, 12 and 13.

In addition to and partly on account of the shortness of the human ilium, in contrast to the ilia of anthropoid apes, the last pair of ribs reaches in man not



This particular index is nearly three times greater in man than in the macaque and considerably greater in man than even in any of the anthropoid apes. Since this proportion, so exceptionally high in man, refers the ilium breadth to the ilium height which has been found to be extremely low in man, it is necessary to

gorilla has also the proportionately broader hips than man (see Fig. 8). The ilium breadth is really a composite dimension, determined by the development in size of its constituent parts: the iliac fossa and the sacral surface. The breadth of the iliac fossa has undergone the most far reaching evolutionary change of any

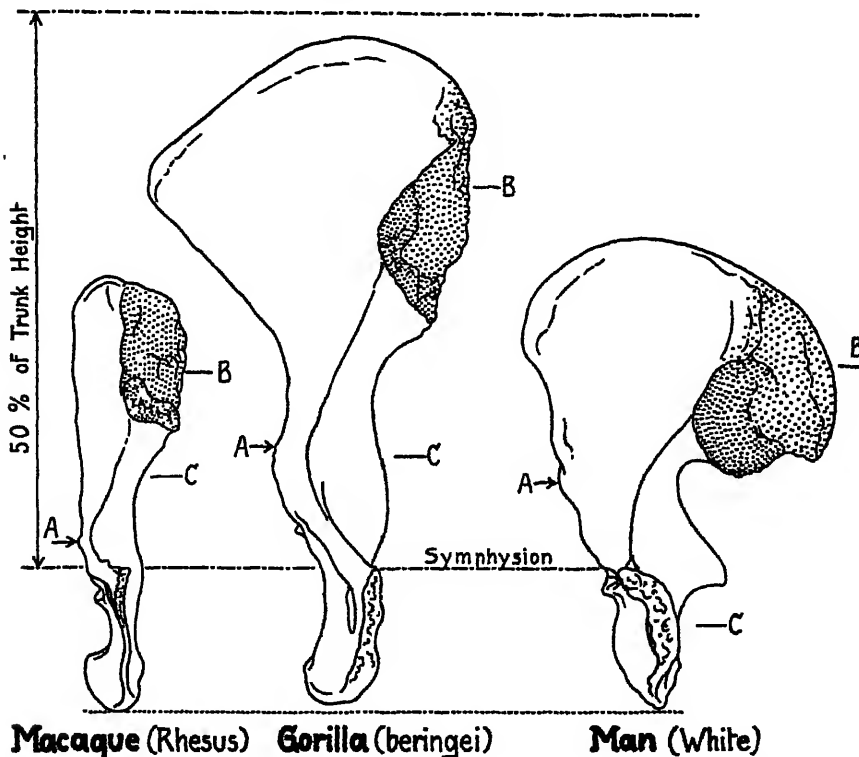


FIG. 11. MEDIAL VIEWS OF RIGHT INNOMINATE BONES OF ADULT MACAQUE, GORILLA, AND MAN

Reduced to the same trunk height, showing relative heights of pelvis and relative sizes of sacral surfaces (dotted areas). A = highest point on acetabulum, B = level of most cranial, ventral, midsagittal point of sacrum; C = level of most caudal, midsagittal point of sacrum. (Drawn with diopetrograph).

analyse the ilium breadth still further. By expressing this breadth first of all in percentage of the trunk height (6th proportion, Fig. 10), it becomes evident that the gorilla possesses an ilium which, in relation to the size of the trunk, is much broader than that of man and that the ilium of the orang-utan is but little narrower. It may be recalled here that the

pelvic dimension in all higher primates. In percentage relation to the trunk height this breadth averages only 5.0 in the macaque, whereas 18.0 in man, 18.5 in chimpanzee, 19.9 in orang-utan, and 27.7 in gorilla. In Figure 10 this index appears, therefore,  $3\frac{1}{2}$  to  $5\frac{1}{2}$  times greater in man and the apes than in the macaque, i.e., this particular proportion deviates



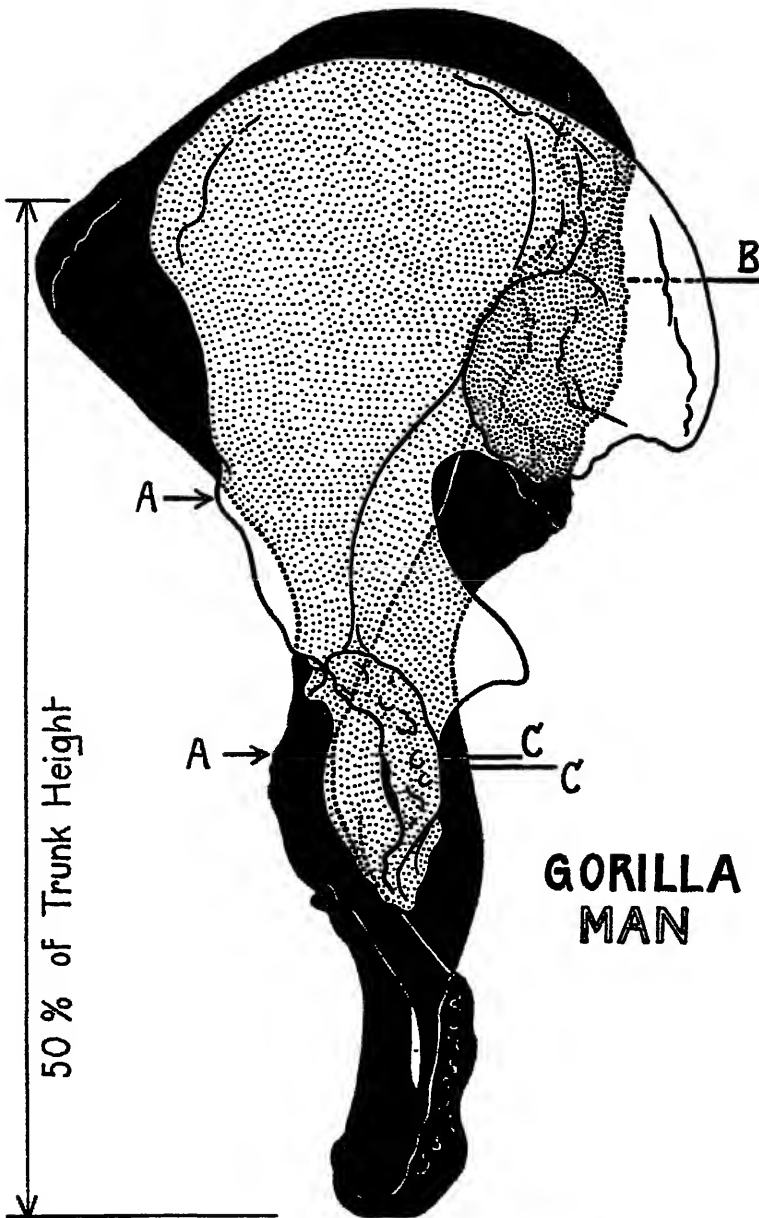


FIG. 12. MEDIAL VIEWS OF RIGHT INNOMINATE BONES OF GORILLA AND OF MAN

Reduced to the same trunk height and superimposed so that the levels of the uppermost, ventral, midsagittal points of the sacra (*B*) and the ventral borders of the sacral surfaces coincide. *A*, *B*, and *C* as in Figure 11. (Drawn with dioptograph).

in the higher primates farther from the primitive condition than any other pelvic proportion in the diagram. It is of special

interest to find that the iliac fossa portion of the ilium is proportionately narrower in man, and hence less specialized, than in

any of the great apes and that, therefore, it must be the sacral portion of the ilium which is so strongly developed in man to produce the great total breadth of the human ilium. In a former paper the author (1930a) had demonstrated that with the acquisition of the erect posture man developed an exceptionally large sacral surface at which the entire weight of the presacral portion of the body is transmitted to the lower limbs. In the brachiators (*Hyloteriidae*, orang-utan and chimpanzee) the sacral surface is consistently somewhat smaller than in the quadrupedal macaque, langur and gorilla. The last proportion in Figure 10 shows clearly all these differences and particularly the exceptional position of man in regard to the relative sacral surface breadth. In the Figures 11 and 12 this enormous development of the sacral surface of the human ilium, produced by new growth in a dorsal direction, is strikingly apparent.

It can now be stated that the unique form of the human ilium is largely the result of the combination between an exceptionally low ilium height and a quite extreme breadth of the sacral surface which is unquestionably an exclusively human specialization.

There exist still other peculiarities in the human pelvis. Its position within the trunk differs fundamentally from the uniform position in the trunks of all other primates, as was shown by the writer (1930a) in a former paper and as is indicated also by the examples in Figure 13.

In the Figures 11 and 12 the levels of the end points of the midsagittal, ventral profile of the sacrum (*B* and *C*) are shown on the drawings of the innominate bones. In the macaque the caudal end of the sacrum lies high above the uppermost point of the *acetabulum* (*A*), in the gorilla at about the same level, but in man far

below the *acetabulum* and, indeed, far below the *symphysis*. This very marked difference, according to which the sacrum reaches in man down to a point opposite the middle of the pubic symphysis, whereas in the gorilla merely to the level of the top of the *acetabulum* and in the macaque even only to a little below the sacral surface of the ilium, plays an important rôle during the act of birth. In macaque and gorilla, as well as in all other

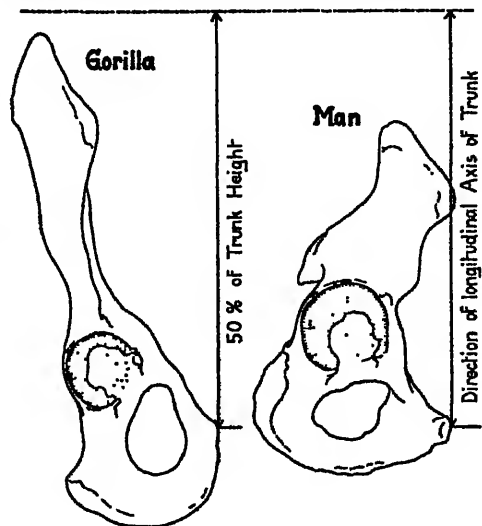


FIG. 13. LATERAL VIEWS (PERPENDICULAR TO PLANE OF ACETABULAR RIM) OF RIGHT INNOMINATE BONE OF GORILLA AND OF MAN

Reduced to the same trunk height, showing difference in size of acetabula. (Drawn with diopetrograph.)

monkeys and apes examined for these conditions, there is no fixed, bony structure opposite the pubic bones, as exists in man in form of the lower part of the sacrum. In the former, therefore, the sacrum interferes not nearly as much with the passage of the fetus to be born, as in the latter.

As shown by Figure 13, the acetabular region of the pelvis is relatively much thicker in man than in the gorilla and the *acetabulum* itself is very much wider in

the former than in the latter. This unquestionably implies that the head of the femur is proportionately larger in bipedal man than in the largely quadrupedal apes. That this conclusion is correct is demonstrated by the data in Table 5. It is seen that man is characterized by the proportionately largest head of the femur among all the primates studied, though the great apes also possess much larger proximal joints on the femora than any of the lower catarrhines. Incidentally, the figures for the relative size of the *caput humeri* indicate that comparatively large

the fact that in all higher primates the *caput humeri* has a diameter from 13 to 25 per cent larger than the diameter of the *caput femoris*, with the one exception of man, in whom the *caput humeri* is invariably much smaller than the *caput femoris*.

After this digression one more differentiating feature of the pelves of higher primates has to be mentioned. As is strikingly evident from the dioptrographic drawings in Figure 14, the iliac fossae of man face one another, i.e., toward the midsagittal plane, whereas in all other higher primates they are pointing practi-

TABLE 5

*The transverse diameters of the caput femoris and of the caput humeri in percentage of the trunk height and the transverse diameter of the caput humeri in percentage of the transverse diameter of the caput femoris in adult primates*

ADULT PRIMATE	SPECIMENS	CAPUT FEMORIS	CAPUT HUMERI	SPECIMENS	CAPUT HUMERI CAPUT FEMORIS
		TRUNK HEIGHT	TRUNK HEIGHT		
Macaque..... . . . .	4	4 3	4 4	4	102.4
Baboon..... . . . .	3	5 4	5 4	5	103.0
Guenon..... . . . .	3	4 0	4 3	3	106.5
Mangabey..... . . . .	2	4 2	4 1	2	98.3
Langur..... . . . .	1	4 8	4 8	1	100.0
Gibbon..... . . . .	1	5.5	6.7	7	113.0
Siamang..... . . . .	.....	.....	.....	3	119.0
Orang-utan..... . . . .	1	7.6	8.8	2	117.3
Chimpanzee..... . . . .	4	7.5	8.6	5	118.7
Gorilla..... . . . .	3	8.2	10.6	9	124.9
Man..... . . . .	15	9.1	8.2	15	89.7

proximal joints are characteristic for the upper as well as the lower extremity in all the higher primates. Since man manifests this general trend even in his upper limbs, it is to be assumed that the large size of his proximal femoral joints has merely become accentuated by the mechanical requirements of bipedal locomotion. The relative size of the proximal joints of the limbs is very evidently not dependent upon the relative lengths of the limbs, but is greatly influenced by body weight, considering also mode of locomotion. The last column of Table 5 reveals

cally in a transverse direction. In the latter the ilia offer very little, if any, direct support for the abdominal viscera, as they do in man, and serve merely as attachment surface for muscles. The enormous development in size of the iliac fossae of the gorilla must have occurred in direct response to the specially great need for increased attachment surface for the powerful musculature of this giant ape, very much as sagittal and occipital crests develop whenever unusually large temporal and nuchal muscles require additional attachment areas.

The pelvis has here been discussed in considerable detail not only because it is a complicated structure which has undergone marked changes in all higher primates, but also because the human pelvis shows many specializations peculiar to man. It is beyond any doubt that in the higher primates the ilium has become remodelled much more profoundly than the other and more uniform pelvic components and that it is chiefly in regard to the ilium that the pelvis of man is separated from the pelvis of any of the anthropoid apes. The distinguishing characters of the human ilium are so numerous and in most instances so very pronounced, whereas the ilia of all the anthropoid apes show so many basic similarities, that no theory which derives man from a gorilla-chimpanzee stock can readily account for these conditions.

The following, very similar conclusion was reached by Straus (1919) from studies dealing with still other features of primate ilia: "The human ilium would seem most easily derived from some primitive member of a preanthropoid group, a form which was lacking in many of the specializations, such as reduction of the iliac tuberosity and anteaacetabular spine and modification of the articular surface, exhibited by the modern great apes. I wish to emphasize here that the anthropoid-ape type of ilium is in no sense intermediate between the human and lower mammalian forms. Its peculiar specializations are quite as definite as those exhibited by man, so that it appears very unlikely that a true anthropoid-ape form of ilium could have been ancestral to the human type."

On the other hand, Reynolds (1931) in a comparative investigation on primate pelvises in relation to the mechanics of erect posture regards the pelvises of the great apes as transitional forms, bridging

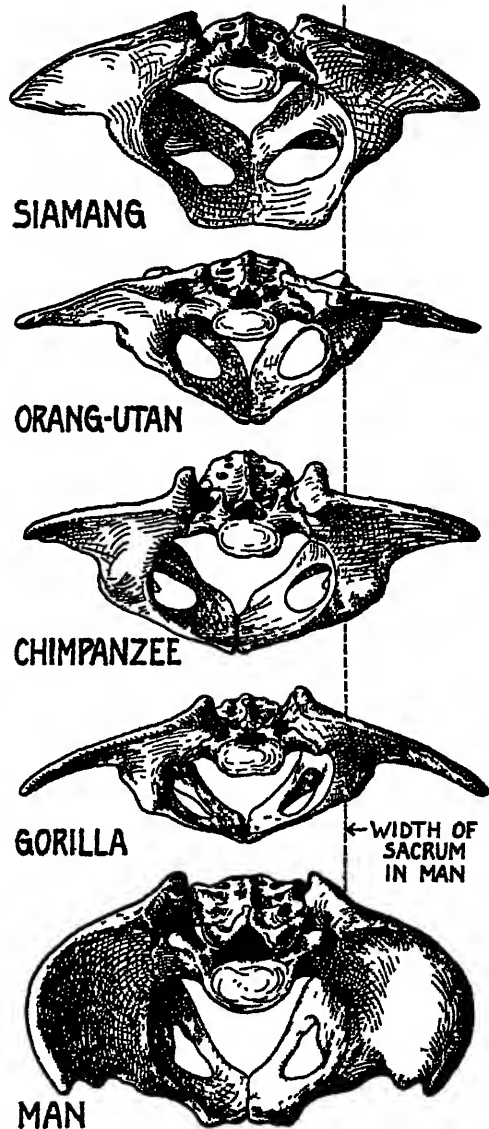


FIG. 14. CRANIAL VIEWS OF PELVES OF ADULT SIAMANG, ORANG-UTAN, CHIMPANZEE, GORILLA, AND MAN

Reduced to approximately the same greatest breadth, showing the curvature of the human ilia and the lack of such curvature in the ilia of the anthropoid apes. (Drawn with dioptrograph.) N.B. There exist marked asymmetries in nearly all of these pelvises.

the gap between the pelvises of lower primates on one side and of man on the

other. Similarly, Gregory (1935) concludes in a rapid survey of the pelvis from fish to man that: "The human pelvis, like the human dentition, jaws, skull, brain, etc., represents the end term of a structural series, the penultimate terms of which are closely approximated in the corresponding parts of the modern African anthropoids." There is, of course, no question in regard to the conclusion that the human pelvis resembles the pelves of the anthropoid apes and, in general, those of the African apes *more* closely than the pelves of any other animals, but, it must be added, there is also no question in regard to the more detailed conclusion that the human pelvis resembles the pelves of the African apes much *less* closely than the anthropoid ape pelves resemble one another. To the writer it appears exceedingly doubtful that the pelvis of the common ancestor of man and the anthropoid apes resembled particularly closely the pelvic type of the recent African apes. This ancestral pelvis can not yet have acquired the extreme specializations common to all recent great apes, nor any of the diverging, fundamental alterations specific for man, but must have been a much more conservative type, approximately intermediate between macaque and chimpanzee. No reasonable allowances for the reversibility of evolution and no ready admission of the profound effects of special mechanical conditions can overcome *all* the many difficulties encountered in an attempt to derive the pelvis of man from that of a chimpanzee-like ape.

#### *Proportions of the Limbs*

The main proportions of the limbs in higher primates have already been described in detail in a special paper by the author (1933b). Some of the results of this previous investigation will here be briefly reviewed with particular emphasis

on the relative differences in limb proportions between lower and higher primates on one hand, and between the various types of the latter on the other hand. These proportions are illustrated by the diagrams in Figure 15.

All higher primates have in common a marked tendency to increase the length of the upper as well as of the lower extremity in proportion to the height of the trunk, but this trend is not yet nearly as evident in newborns as in adults. It is particularly noteworthy that not only man, but also the anthropoid apes, possess relatively longer lower extremities than the macaque and that not only the anthropoid apes, but also man, have proportionately longer upper extremities than the macaque and other lower catarrhines, at least at the completion of growth. In regard to the relative length of the lower limb, man represents the maximum, and in regard to the relative length of the upper limb the minimum degree of specialization among the higher primates, but nevertheless he belongs clearly in this group on the basis of both these limb proportions. The ranges of individual variations in these relative limb lengths can in rare cases overlap in man and some anthropoid apes. For instance, the relative lower limb length amounts to only 151 in an adult Hawaiian, whereas to 153 in two adult gibbons and the relative upper limb length equals 174 in an adult Negro, but only 148 and 160 in two adult mountain gorillas and 166, 168 and 173 in three adult chimpanzees (Schultz, 1933b). No adult man, however, has ever been found who possesses at the same time as long an upper *and* as short a lower limb length as any anthropoid ape.

The average relative lower limb length in adult man is slightly over 75 per cent greater than in adult macaques, but the relative upper limb length in adult gibbons



the forearm and the upper arm, ranges among lower catarrhines only between 97 and 105, whereas among higher primates between 70 and 118 (Schultz, 1933b). On an average man possesses the lowest brachial index of all simian primates at birth as well as in adult life, but in some lowland gorillas the forearm is proportionately shorter than in many Negroes. It is of great significance also that differences in this proportion between the various primates studied are not yet nearly as pronounced at birth as in adult life. The same increase in generic differences with advancing postnatal growth exists also in the other limb proportions shown in Figure 15.

Among all lower catarrhines and, most probably, in the common ancestor of higher primates the radius has approximately the same length as the humerus. The extreme shortening in the relative length of the radius, characteristic of man and the lowland gorilla, represents unquestionably a new phylogenetic acquisition, having appeared independently in the two. The nearly as extreme change from the original condition in an opposite direction, i.e., the great proportionate lengthening of the radius, most pronounced in the gibbons, must also be regarded as a new specialization.

In regard to these limb proportions adult man is least removed from the gibbon in one instance, from the mountain gorilla in two instances, and from the lowland gorilla in the remaining instance. The differences in the proportions appertaining to the upper extremity (relative length of upper limb and brachial index) are smaller between man and one or the other gorilla than between the particular gorilla and chimpanzee, but the differences in the proportions based upon the lower extremity (relative length of lower limb and intermembral index) are larger be-

tween man and the nearest anthropoid ape (gibbon and gorilla respectively) than even between gibbon and gorilla. It can be concluded, therefore, that in regard to the proportions of his upper extremity man stands very close to some anthropoid apes, whereas in the proportions of his lower extremities he has become far removed from all other higher primates.

#### *Proportions of Hand*

The differences between various primates in regard to the proportions of the hand are shown in Figure 16. In relation to the trunk height the hand length is greater in all adult higher primates than in adult macaques, but the degrees of this phylogenetic lengthening of the distal segment of the arm differ very significantly in the various genera. The proportionately shortest hand is found in the mountain gorilla; man possesses the second shortest hand, whereas the relatively longest hands occur in the most extreme brachiators, the orang-utan and gibbons. For some, as yet not clearly understood reason the relative hand length as well as the relative foot length is exceptionally short in newborn man, in contrast to the newborns of other higher primates.

If the length of the hand is expressed in percentage of the length of the proximal and middle segments of the upper extremity, it is found that chimpanzee and orang-utan have much higher indices than the siamang and gorilla, while man occupies an intermediate position in this respect. This indicates that an increase in the relative total length of the upper limb (see Fig. 15) does not necessarily affect the length of the hand to anywhere near the same degree. For instance, the total upper limb length in relation to the trunk height averages in lower catarrhines 118 and in siamangs it has increased to 233, but the hand length in relation to the

combined lengths of forearm and upper arm averages in the former 35 and in the latter only 28. Man and gorilla are distinguished by the shortest hands of all higher primates not only in relation to the trunk height but also in relation to the limb length, and in the mountain gorilla the hands are proportionately even shorter than in man. (For further details on this and the following hand proportions see Schultz, 1933b).

Among newborns man possesses the highest relative hand breadth; this is most probably due to the exceptional shortness of the hand in newborn man. The relative hand breadth decreases in general with age in man and all other primates studied (Schultz, 1926), except in the gorilla in which the hand is still comparatively slender during middle fetal life (see, e.g., Schultz, 1927, Plate V). If it is concluded from this that the ex-

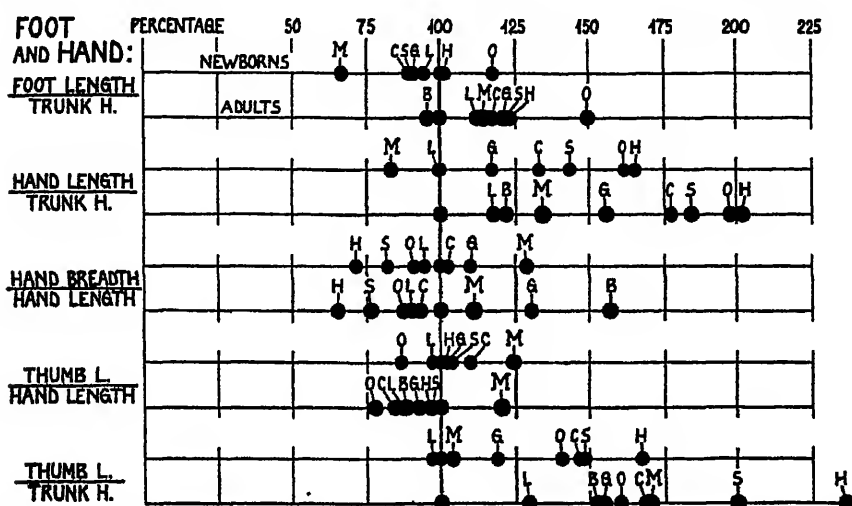


FIG. 16. DIAGRAMMATIC REPRESENTATION OF THE RELATIVE FOOT LENGTH AND SOME PROPORTIONS OF THE HAND IN NEWBORN AND IN ADULT HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING PROPORTIONS IN NEWBORN AND IN ADULT MACAQUE

For explanation of abbreviations see title of Figure 7.

The adult *Hylobatidae*, orang-utan and chimpanzee have proportionately narrower hands than the macaque, whereas man and, particularly, the two species of gorilla have developed much broader hands (Fig. 16, third proportion). As in the brachial index, so in this hand index there clearly exist divergent evolutionary trends among the higher primates. The gibbon with a relative hand breadth of only 23.8 (average of 16 adults) represents one extreme and the mountain gorilla with an average index of 58.5 the opposite extreme.

The extreme breadth of the gorilla hand is a late phylogenetic acquisition, as it is a late ontogenetic one, it must be assumed consistently that man developed the second broadest and shortest hand at a comparatively early stage of his evolution and has probably never possessed the typically long and slender brachiator's hand.

In relation to the length of the hand the total length of the thumb is greater in man than in the macaque, whereas shorter in all the anthropoid apes (Fig. 16, fourth proportion). At first glance this difference between man and the anthropoid apes



is so striking that it is sometimes asserted that the thumbs of the latter have become atrophied in consequence of their arboreal habits (e.g., Clark, 1935) or that the thumb of man has undergone a decided lengthening (e.g., Gregory, 1934). Since, however, the length of the hand in general has undergone changes with widely differing intensity, it is evident that the thumb length should be compared not only with the frequently changed hand length, but also with an independent measure, such as the trunk height. According to the latter relation (Fig. 16, fifth proportion) all adult higher primates possess really much longer thumbs than the macaque, and man stands in this respect in the midst of the anthropoid apes. It is thus possible to be more precise by stating that in proportion to their body size all higher primates have actually longer thumbs than the lower catarrhines and that it is only due to the widely differing increases in hand length that the thumb merely appears to be short in the apes, whereas long in man. For instance, in an adult chimpanzee and an adult man, measured by the author, the thumb length equals 24 per cent of the trunk height in both, but the hand length amounts to 53 per cent of the trunk height in the former and only to 36 per cent in the latter. It is to be expected, therefore, that in relation to the widely differing hand lengths the thumb length is also very different in the two, namely 46 in the chimpanzee, whereas 68 in man.

Another factor has to be considered in connection with a discussion of the length of the thumb and that is the relative length of the free portion of the thumb beyond its place of branching from the palm. Only in the *Hylobatidae* does the "free thumb" include a large part of the first metacarpal bone, whereas in some gorillas only the distal part of the basal

phalanx belongs properly to the free portion of the thumb. According to Midlo (1934), who has studied this question in detail, the free length of the first digit in percentage of the palm length amounts on an average to 70 in *Hylobatidae*, to 56 in man, to 44 in the chimpanzee, to 40 in the lowland gorilla, and to 34 in the orang-utan; i.e., the part of the thumb not included in the palm is proportionately much longer in gibbons and siamangs than in man. In the former the total length of the thumb is also much longer in relation to the trunk than in the latter (Fig. 16, last proportion) and the thumb of the *Hylobatidae* branches from the palm at a place much nearer to the wrist than in any other primate (Schultz, 1933a and Midlo, 1934). It is seen, therefore, that the thumbs of the gibbons and the siamangs are in several important respects more highly specialized than the thumbs of man or of the great apes.

Among all higher primates the thumb length in proportion to the hand length is longer in fetuses than in adults. This ontogenetic decrease is much more pronounced in chimpanzees than in man and this chiefly on account of the differences in the growth changes of the relative lengths of the hands.

The rotation of the thumb, by which the first digit has come to face the lateral fingers even when adducted, is little developed in the lower catarrhines in contrast to the higher ones and is not yet present in early fetal life of any primate. Among adult higher primates this rotation, which greatly facilitates the complete opposability of the thumb, is even more advanced in some chimpanzees than in the average man (see e.g. Schultz, 1931b, Fig. 22).

In all lower catarrhines, all orang-utans, and the large majority of the African apes the second finger is significantly shorter

than the fourth. In an exceptional chimpanzee or gorilla these two fingers may be equally long. In man the second finger surpasses the fourth in length in many Whites and in small percentages of Negroes and of Indians (Steggerda and Millar, 1936). Among the *Hylobatidae* a second finger, longer than the fourth, is particularly common, having been found in 19 out of 49 gibbons and in 10 out of 14 siamangs (Schultz, 1933a). In this respect, therefore, man and the *Hylobatidae* are unique among all the primates, since in platyrrhines and prosimians the difference between the two digits in favor of the fourth is even greater than in most catarrhines.

It is also noteworthy that the proportions between the lengths of the metacarpi and the phalanges have remained practically unaltered in the various higher primates (Schultz, 1930a, Table 30) by the radical changes in the relative length of the hand or in that of the thumb. It will be shown in the following chapter that in this respect the foot is strikingly different. It will also be demonstrated that among the higher primates the foot is not nearly as conservative and comparatively uniform as the hand, but has undergone much more far reaching specializations in connection with such different modes of locomotion as exist, e.g., in orang-utan and man.

*Proportions of the Outer Foot and of the Foot Skeleton*

The foot in proportion to the trunk is longer in adult higher primates than in the adult macaque, with the exception of the mountain gorilla (Fig. 16, first proportion). The extreme in relative foot length has been attained by the orang-utan, and man stands in this respect between langur and chimpanzee. The ex-

ceptionally short relative foot length of the mountain gorilla is compensated for by the greatest relative foot breadth among all simian primates. The second highest relative foot breadth is found in the lowland gorilla and the third in the chimpanzee. Man ranks fourth in this proportion, i.e., the human foot (without digit I) is narrower than the foot of the African apes and is more similar in length-width proportion to the feet of lower catarrhines (Schultz, 1933b).

As stated above, man and chimpanzee have practically the same foot lengths in relation to their trunk heights. In man, however, 49 per cent of the foot length belong to the tarsus, whereas in the chimpanzee only 35 per cent, and 21 per cent of the human foot length represent the phalangeal portion of the middle toe in contrast to 36 per cent in the chimpanzee (Schultz, 1930a, Table 31). It is evident that the relative foot length by itself and comparative data on the proportions of the foot skeleton alone are insufficient for a full comprehension of the phylogenetic changes which must have taken place in the relations between the lengths of the various elements of the foot skeleton. It is necessary to correlate the size of tarsus, metatarsus and phalanges with the general size of the animal, as represented by the trunk height. These correlations are shown in Figure 17. The first proportion expresses the length of the tarsus in percentage of the trunk height. It is seen at once that man is characterized by the relatively largest tarsus, though in the gorilla the tarsus is but little smaller than the average of man and equally large as some individual human variations (see e.g. Fig. 19). The length of the metatarsal region in relation to the trunk height is larger in all higher primates than in the macaque and differs comparatively little among the former. The length of the

middle metatarsal bone is also quite uniform in its relation to the total length of metatarsal region is the most constant

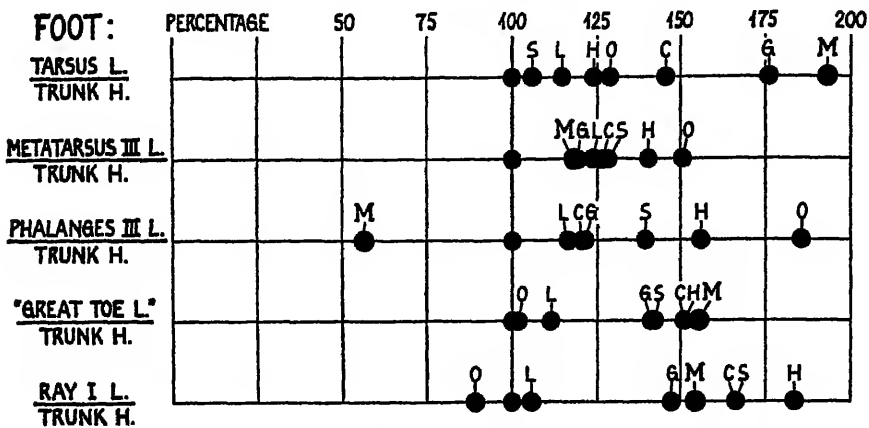


FIG. 17. DIAGRAMMATIC REPRESENTATION OF SOME PROPORTIONS OF THE OUTER FOOT AND OF THE FOOT SKELETON IN ADULT HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING PROPORTIONS IN ADULT MACAQUE

The data used for this figure are based upon as yet only partly published measurements by the author taken on the same adult specimens, as listed in the title of Figure 9. Measuring technique of foot skeleton discussed in another paper by the author (1930a). For explanation of abbreviations see title of Figure 7.

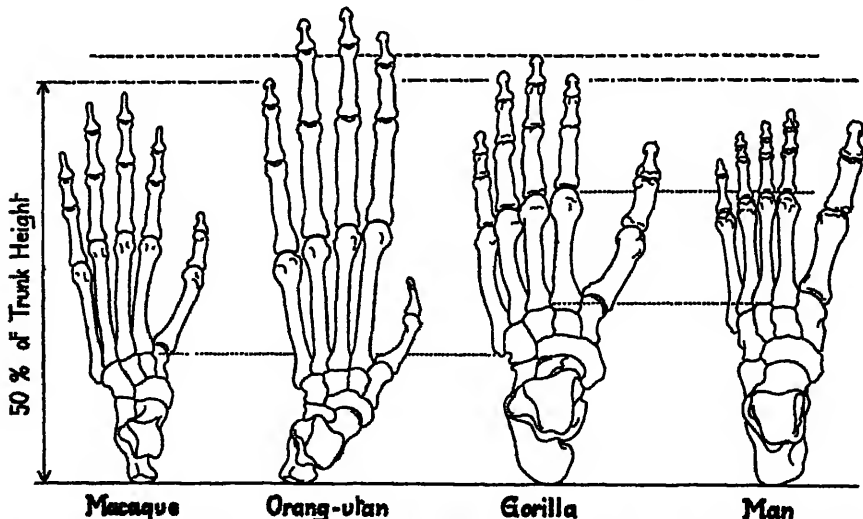


FIG. 18. FOOT SKELETONS OF ADULT MALE MACAQUE (RHEBUS), ORANG-UTAN, LOWLAND GORILLA, AND MAN (HAWAIIAN)

All reduced to the same trunk height. (Drawn with dioptrograph)

the foot skeleton in man and all anthropoid apes, but this proportion is somewhat smaller in the higher than in the lower part of the foot skeleton is also readily seen by the examples in Figure 18. The length of the third segment com-

posing the total foot length, or the phalangeal portion, differs widely among higher primates not only in relation to the length of the tarsal and metatarsal region, but also in relation to the height of the trunk (Fig. 17, third proportion). In regard to both these relative measurements man represents one extreme and the orang-utan the opposite extreme, i.e., man has by far the shortest and the orang-utan the longest phalanges not only in relation to the total foot length, but also in proportion to the size of the body; indeed, these are the most extreme specializations in phalangeal length among all the many simian primates examined by the author.

The foot skeleton of the orang-utan is characterized by one of the shortest tarsal portions among higher primates in addition to the longest phalangeal portion, whereas the corresponding human peculiarities consist in a combination of the longest tarsus and shortest phalanges. This tremendous difference is most strikingly shown by the percentage relation between the length of the phalanges (III) and that of the tarsus, which averages only 43 in man, whereas 166 in orang-utan. It is significant in this connection that this same proportion still amounts to 89 in human fetuses of the tenth week, i.e., to nearly as much as in the adult chimpanzee with an average of 101 (Schultz, 1930a, Table 32).

The unique phylogenetic shortening of the phalangeal portion of the toes in the only true bipedal primate, man, has affected most of all the middle phalanges, which form only 24 per cent of the total phalangeal length (III) in man, whereas roughly 33 per cent in orang-utan, the *Hylotidae* and most lower catarrhines (Schultz, 1930a, Table 33; see also Fig. 18). Furthermore, only in man does one encounter the complete lack or, at least, the fusion with the distal phalanx of the

middle phalanx of, particularly, the fifth toe, a condition already occurring in a majority of the cases in some human races.

In man alone does the great toe reach as far as, or even farther than, any of the other toes, at least during postnatal life. From this many authors have concluded even in recent times that the great toe of man has become longer, or has hypertrophied in general (e.g. Clark, 1935 and Gieseler, 1936). However, Schwalbe (1916), Virchow (1917), Weidenreich (1921) and the author (1930a) have already pointed out that it is not the great toe of man which has become longer, but the lateral toes II to V which have become shorter. If the great toe length (from heel to tip of great toe) is expressed in percentage of the trunk height (Fig. 17, fourth proportion), man stands most removed from the macaque, but gibbon and chimpanzee are very close to man in this respect. The "great toe length," as used on the outer foot, is composed in the skeleton of the tarsal length in addition to the length of the first digital ray. The latter length by itself equals exactly 100 per cent of the former length in man, whereas 122 per cent in chimpanzee (Schultz, 1930a, Table 32). If, therefore, the length of only ray I is expressed in relation to the trunk height (Fig. 17, last proportion), it is found that, considering the size of the animal, gibbon, siamang and chimpanzee possess actually longer great toes (phalanges + metatarsus I) than does man. That the human hallux is but very little longer than the hallux of the gorilla, when both have been reduced to comparable size of the trunk, is clearly shown by Figure 19. The same figure, as well as a comparison between the various foot proportions in Figure 17, demonstrates beyond any doubt that the most striking morphological distinction between the foot skeletons of man and

gorilla consist in the different relative lengths of the phalanges of the lateral toes. The human specialization in this respect does not diverge any more in one direction than do the peculiarities of the orang-utan foot in the opposite direction.

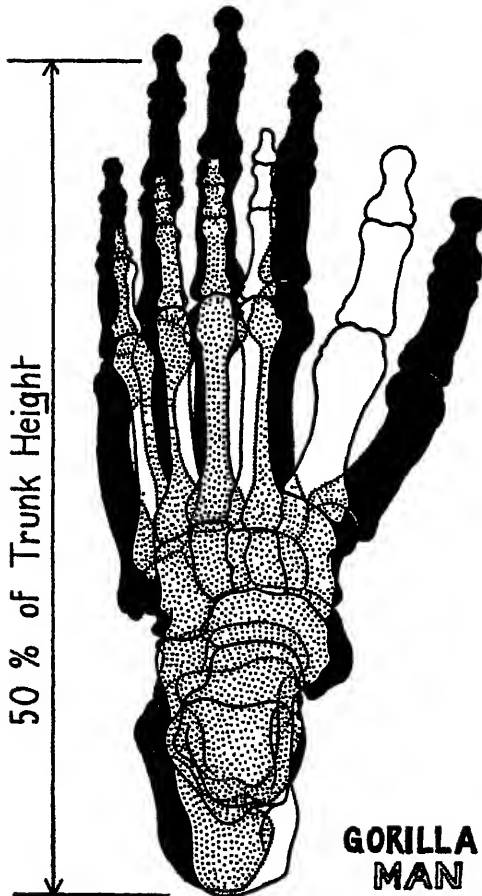


FIG. 19. FOOT SKELETONS OF THE ADULT GORILLA AND MAN, shown in Figure 18, SUPERIMPOSED. Reduced to same trunk height. (Drawn with di-optograph.)

The latter are most evident in the great length of the phalangeal portion of the lateral toes and in the striking reduction, amounting to a degeneration, of the hallux (see Fig. 18). In many orang-utans the terminal phalanx and the nail of the great

toe is missing, just as in man the middle phalanx of the reduced fifth toe is frequently absent and the nail rudimentary or also lacking. These marked reductions of the great toe in orang-utan are already present in fetal life and are hence not due to self-mutilation, as suggested by Yerkes and Yerkes (1929, p. 107). The degenerate great toe of orang-utan has lost the faculty of complete adduction in many old individuals, but can be abducted much farther than in the gorilla. The great toe of man with its opposite specializations has lost the power of, at least metatarsal, abduction, though the joint at its base still shows unmistakable traces of former movability (Schultz, 1930a, Fig. 22).

The proportions and the skeletal parts of the foot of man can readily be explained as modifications of a generalized and conservative anthropoid ape type of foot. A very similar conclusion has been reached in regard to the mechanical construction of the foot by Morton (1927) and by Elftman and Manter (1935). Many fetal growth changes in the human foot also support this view (Schultz, 1926). It must be emphasized, however, that in all these conditions the differences between the foot of man and the generally most similar foot, that of the gorilla, are far greater than the differences between the feet of gorilla and chimpanzee.

In regard to the foot musculature the gap between man and the anthropoid apes is apparently considerably greater than that existing in regard to the skeleton and the proportions. Thus, Wells (1931) concludes: "The fact that the soft anatomy of the human, and especially of the Bantu foot, is less differentiated from a generalized type than that of the foot of the anthropoid apes, so as to present a surprising resemblance to that of the baboon's foot, indicates that the separation of the

human from the simian stem took place when both were but little differentiated from the ancestral catarrhine stock, from which the Cercopithecidae also arose." Based upon his extensive studies on the foot musculature in primates, published in 1930, and upon many later, additional observations Dr. W. L. Straus, Jr. has reached essentially the following conclusions, which he has kindly permitted to be mentioned here: If the foot musculature as a whole is considered, the gorilla resembles man more closely than does any other primate. In certain important muscular details, however, the human foot is much more primitive and generalized than are the feet of gorilla and other anthropoid apes and approaches the conditions in lower catarrhines. The foot musculature of man is most easily derived from a type which in its general plan differed but little from that found in the lower catarrhines. From this ancestral type the resemblances between man and the anthropoid apes resulted by parallel and independent trends.

#### *Proportions of the Head*

The relative differences between the various primates studied in regard to some of the proportions of the head are illustrated in Figure 20. All the higher primates possess relatively larger heads than the macaque and this already at birth. Among the new-borns orang-utan and gibbon have the proportionately larger heads than man (see chapter on relative cranial capacity, notes on newborns), but during postnatal life the head of man continues to increase in size more intensively and for a longer period than in the anthropoid apes, so that man acquires the relatively largest head among adults.

The relation between the total face height and the trunk height removes man from the large apes, inasmuch as all the

latter have proportionately much larger faces than the former. At birth the *Hylobatidae* possess in relation to the size of their trunks a higher face than man, but in adults this proportion has become somewhat greater in man than in gibbons and siamangs on account of a less pronounced postnatal growth change in the former than in the latter.

In proportion to the size of the brain part of the head the face part is smaller in man than in any of the other primates studied (Fig. 20, third proportion), a difference even more marked at birth than at the completion of growth. The unique position of man in regard to this particular index is to be expected, since it is man among all higher primates in whom the largest brain part is combined with one of the smallest face parts of the head.

Man possesses at all ages a comparatively broad interocular region, indeed, among adults he surpasses in this respect all other higher primates (Fig. 20, fourth proportion). The gibbon approaches man most closely in regard to this relative distance between the eyes. It may be mentioned here that, according to comparative anatomical and growth studies, a broad interocular region must be regarded as a primitive character. Hence the orang-utan with its extremely narrow width between the eyes is more highly specialized than man with his broad width, though the latter is more advantageous for stereoscopic vision.

The relative size of the outer ear (ear height  $\times$  ear breadth in percentage of head length  $\times$  total head height; Fig. 20, fifth proportion) varies very extensively among higher primates, namely between only 2.5 in some adult orang-utans and 20.3 in some adult chimpanzees. In the latter the ears have become greatly overdeveloped, whereas in the former they have degenerated to the smallest relative

size among all primates. The same proportion varies among adult lower catarrhines only between about 9 and 19. The relative ear size furnishes one more of the many examples in support of the general claim that, in comparison with the numerous and uniform lower catarrhines, the few types of higher primates are characterized by a conspicuous facility

indicated, little more of the helix being bent over than in the lower catarrhines (Schultz, 1931b and 1933a). A true and large ear lobule, free of cartilage, is found only in the majority of human beings and in some chimpanzees and gorillas.

Among the adult higher primates man stands nearest to the gorilla in regard to relative head size and relative ear size,

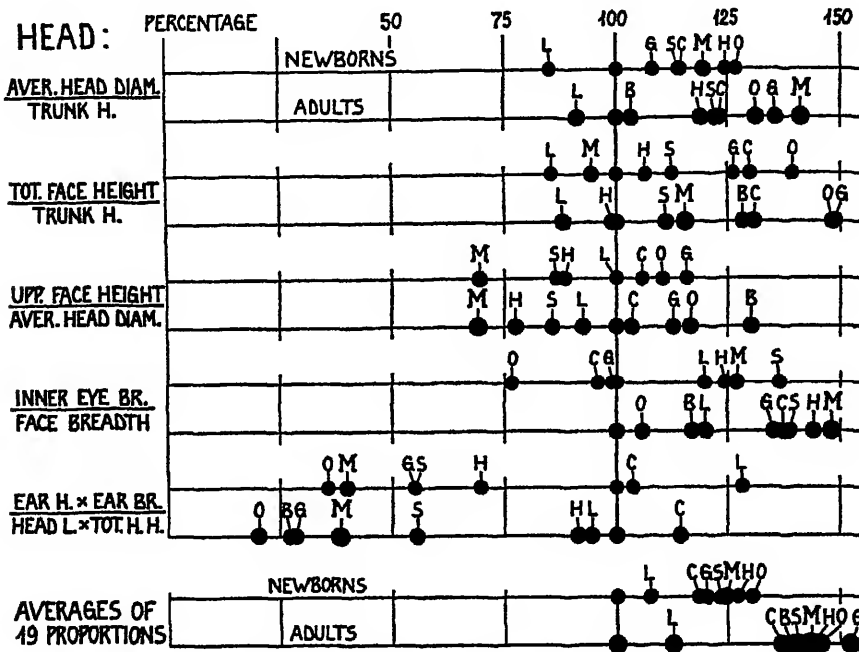


FIG. 20. DIAGRAMMATIC REPRESENTATION OF THE MOST SIGNIFICANT PROPORTIONS OF THE HEAD AND AVERAGES OF ALL THE BODY PROPORTIONS (in the Figures 8, 15, 16, and 20) IN NEWBORN AND IN ADULT HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING PROPORTIONS AND AVERAGES IN NEWBORN AND IN ADULT MACAQUE

For explanation of abbreviations see title of Figure 7

for far reaching and widely divergent specializations.

The higher primates have in common a marked tendency for the free edge of the ear (*helix*) to become rolled in during postnatal growth. This is decidedly most pronounced in gibbons and siamangs and is also very evident in orang-utans, gorillas and most human races. In chimpanzees, however, this trend is usually only

nearest to the gibbon in regard to relative upper face height and relative interocular width, and nearest to the siamang in regard to relative total face height.

#### *Average Generic Differences in Regard to Proportions of Outer Body*

Some strictly limited, yet very significant and condensed information can be gained from a study of the *average* relative

differences between the higher and lower catarrhines in regard to all the proportions, appertaining to the outer body, discussed in this paper (see Fig. 20, bottom). These averages disregard quite properly whether a particular deviation from the condition in the macaque falls on the right or on the left of the line representing the macaque; in other words, the absolute differences between corresponding proportions in higher primates and macaque (and not the absolute values in the former) are expressed in percentage of the values in the latter regardless of *plus* or *minus* sign, since these *averages* are intended to show merely the relative amounts of the general differences, but naturally not the direction of these differences.

Among adults the particular body proportions considered here differ on a general average from the same proportions in the macaque by the following percentages of the values in the macaque: Langur = 12.7; chimpanzee = 37.2; mountain gorilla = 39.2; siamang = 40.8; man = 43.4; gibbon = 43.9; orang-utan = 45.7; lowland gorilla = 52.0. These figures demonstrate first of all that *all* higher primates differ much more from the macaque than the latter representative of the subfamily *Cercopithecinae* differs from the langur, representing the subfamily *Semnopithecinae*. In regard to the general average of his body proportions man stands in the midst of the anthropoid apes and this among adults as well as among newborns. Several of the apes have in general deviated farther from the conditions in the lower catarrhines than has man. As shown by a glance at Figure 20, all higher primates and the langur stand in regard to the aggregate condition of their body proportions much closer to the macaque at birth than at the completion of growth. This result could not be expected without the

conclusion that all higher primates developed from some common ancestor which closely resembled the conservative forms among the recent lower catarrhines and from which the latter as well as the former inherited the same plan of growth which later became altered here or there by gradually increasing ontogenetic modifications producing the diverging, phylogenetic specializations.

#### SUMMARY AND CONCLUSIONS

Most of the specific and detailed data collected and discussed in this paper are enumerated in a very condensed manner in Table 6, which serves as a convenient summary and as a general basis for the following conclusions.

The group of higher primates is characterized first of all by its striking plasticity as manifested by its enormous generic variability in contrast to the comparative uniformity among the lower catarrhines. This difference becomes particularly impressive when it is recalled that (chiefly according to Elliot, 1913) the family *Cercopithecidae* consists of 16 recent genera and approximately 260 species, whereas the higher primates are composed of only 6 recent genera containing at most 28 species. It is with the few higher primates that evolution has made the most far reaching experiments, carrying them not only to widely differing levels along the same directions, but also in many respects in greatly diverging directions. The multitudinous Old World monkeys, on the other hand, represent as a whole a remarkably homogeneous and fairly primitive group regarding their fundamental anatomical characters, when compared with the remaining catarrhines, the anthropoid apes and man. That the *Cercopithecidae* have in general been content with minor specializations and that the higher primates alone have possessed the





Frontal Sinuses.....	absent.....	absent.....	small sin- uses pre- sent in some cases	generally large, oc- casionally very small	always very large*	small to large, oc- casionally lacking
Os centrale of Wrist fused with Os naviculare.....	never.....	frequently in old age.....	occasionally in old age	in late fetal or even infantile life	in an infant of 3-5 years not yet fused	during 3rd fetal month*
Nasal Bones fuse in.....	fetal life.....	Juvenile life (after crup- tion of M1)	Juvenile life	Juvenile life, rarely in sub-adults	Juvenile life, sometimes in sub-adults	only in old age in very rare cases*
Average Total Number of Vertebrae.....	48.9.....	32.1.....	30.8*	32.6.....	32.3.....	33.4.....
Average Number of Thoracolumbar Vertebrae.....	18.9.....	17.9.....	16.6*	16.8.....	16.6.....	17.0.....
Average Number of Sacral Vertebrae.....	3.0.....	4.4.....	5.1.....	5.4.....	5.6*	5.2.....
Average Number of Coccygeal Vertebrae.....	ca. 17.0.....	2.7.....	2.8.....	3.2.....	3.0.....	4.2.....
Length of Cervical Region of Spine in % of Trunk Height.....	18.....	17.....	24.....	23.....	24.....	26*
Length of Lumbar Region of Spine in % of Trunk Height.....	45.....	25.....	24.....	17*	28.....	37.....
Proportionate Distance between last Ribs and Iliac Crests of Pelvis.....	very long.....	medium.....	very short.....	very short.....	extremely short*	medium.....
Chest Girth in % of Trunk Height.....	103.....	149.....	185.....	176.....	223*	162.....
Shoulder Breadth in % of Trunk Height.....	35.....	53.....	59.....	57.....	72*	67.....
Hip Breadth in % of Trunk Height.....	33.....	43.....	50.....	55.....	67*	58.....
Chest Breadth in % of Chest Depth.....	87.....	118.....	126.....	119.....	135.....	129.....
Height of Shoulder (above suprasternal notch) in % of Trunk Height.....	5.....	12.....	16.....	17**.....	13.....	2**.....
Height of Nipples (above Symphysis) in % of Trunk Height.....	80.....	84.....	90**.....	86.....	82.....	76**.....
Width between Nipples in % of Chest Breadth.....	40.....	32.....	89**.....	52.....	46.....	71.....
Total lower Limb Length in % of Trunk Height.....	96.....	147.....	119.....	128.....	131.....	171*
Total upper Limb Length in % of Trunk Height.....	107.....	238*.....	182.....	175.....	184.....	150.....
Total lower Limb Length in % of Total lower Limb Length.....	111.....	162.....	170.....	137.....	140.....	88**.....

TABLE 6—Continued

CHARACTER	LOWER CAVAL- RIDERS c. s. Males	HYLOBATIDAE		ORANG-UTAN	CHIMPANZEE	GORILLAS		MAN
		Gibbon	Siamese			Lowland	Highland	
Diameter of Caput humeri in % of Diam. of Caput femoris.....	100.	113	119	117	119	125**	125**	90**
Forearm Length in % of Upper arm Length.....	97	113**	107	101	90	78	83	77**
Hand Length in % of Trunk Height.....	28	56*	51	55	49	43	34	37
Hand Breadth in % of Hand Length.....	37	24**	29	33	35	49	58**	41
Thumb Length in % of Trunk Height.....	14	34*	29	23	24	22	22	24
Thumb Length in % of Hand Length.....	56	54	55	44**	47	52	50	68**
Free Length of Thumb in % of Palm Length (Midlo).	30	72*	68	34	44	40	35	56
Relative Position of Place of branching of Thumb from Palm (Midlo).....	66	30*	40	45	44	59		55
Foot Length in % of Trunk Height.....	43	53	52	64*	50	52	41	49
Great Toe Length (from heel) in % of Trunk Height.....	31	47	44	31	46	44	44	48*
Length of Phalanges + Metatarsus I in % of Trunk Height.....	15	27**	24	13**	24		22	23
Length of Phalanges of Toe III in % of Trunk Height.....	15	23	20	27**	18		18	8**
Tarsus Length in % of Trunk Height.....	12	15	13	16	18		21	23*
Average Head Diameter in % of Trunk Height.....	21	26	26	28	26	29	22	30*
Total Face Height in % of Trunk Height.....	21	21	23	31*	27	31*	27	24
Upper Face Height in % of Average Head Diameter.....	73	56	62	85	75	82	95**	50**
Inner Eye Breadth in % of Face Breadth.....	17	25	24	18*	23	23	20	25
Relative Ear Size.....	14	13	8	3**	16**	4	4	5
Breadth of Mandibulum sterni in % of Trunk Height.....	6	11	10	12	11		15*	12
Breadth of Corpus sterni in % of Length of Corpus sterni.....	13	39	53	58*	21		45	38
Ilium Height in % of Trunk Height.....	25	32	35	36	39		40*	25
Ilium Breadth in % of Ilium Height.....	41	46	60	72	60		90	122*
Ilium Breadth in % of Trunk Height.....	15	15	21	26	23		36*	30
Iliac Fossa Breadth in % of Trunk Height.....	5	11	15	20	19		28*	18
Sacral Surface Breadth in % of Trunk Height.....	6	5	6	6	6		8	12*
Fossa Iliaca facing.....	ventrally	ventrally	ventrally	ventrally	ventrally	ventrally	ventrally	sagittally*

\* = highest degree of specialization; \*\* = highest degree of divergent specializations.

capacity for many radically new developments can here be illustrated by merely a few random examples. In spite of the fact that the *Cercopithecidae* include ten times more species than the higher primates, the number of true sacral vertebrae is practically always the same among the former (i.e., 3; 2 or 4 vertebrae occurring in only very rare instances), but among the latter this number fluctuates widely between 3 and 7. The relation in length between the upper and lower limbs (intermembral index) varies among adult Old World monkeys only between 104 and 123, whereas among the higher primates between 85 and 183. In all lower catarrhines the permanent canine teeth are large in males and small in females. Only among the higher primates have changes in this sex difference occurred and this even in opposite directions, namely in the gibbons and siamangs in which the canines are very large in both sexes, and in man in whom the canines are small in females and in males. Large throat pouches are unknown among all lower catarrhines, but are developed to an enormous size in siamangs and orang-utans. The body weight of normal adults ranges among the catarrhine monkeys from about 2 kg. in a talapoin to hardly more than 35 kg. in some male baboons, but among the higher primates it varies between 4 kg. in some gibbons and over 250 kg. in male gorillas. There exist far greater differences in the shape of the foot between man and orang-utan or in the size of the outer ear between chimpanzee and orang-utan than have been found in these characters among all the lower catarrhines. Among the latter the mode of locomotion is always chiefly quadrupedal, whether on the ground or in the trees, and exclusive brachiation is rarely and quite temporarily resorted to. In the higher primates alone have new modes of locomotion developed, namely

the erect bipedal walk of man, the rather clumsy bipedal trot of gibbons, the extreme and highly perfected brachiation of the slow orang-utans and the rapid *Hyloteropidae*, and the quadrupedal walk on the horny knuckles of the flexed fingers of the African apes.

On account of this first, and perhaps most important, common character of higher primates—their great plasticity or faculty for modifications—this group contains many divergent specializations. In spite of the latter the higher primates can properly be regarded as one natural group, because not only are they all separated from the lower catarrhines, but they also all share a great many evolutionary trends, as is manifested by those countless phylogenetic alterations which are identically directed in all, differing only in the degrees of perfection attained by the various types. Of the sixty characters listed in Table 6, sixteen have developed in divergent directions among the higher primates, but the remaining great majority contains many conditions which reveal definite single trends in all anthropoid apes and man. Of such common trends the following may be specially mentioned as outstanding examples (see also Table 6). Contrasted with lower catarrhines all higher primates have in common: Prolongations of the duration of pregnancy and the total period of postnatal growth (as far as known); the gradual disappearance of ischial callosities; a widely varying tendency for fusion of the *os centrale* with the *naviculars*; a tendency for late fusion between the nasal bones; reductions in the total number of vertebrae and in the numbers of thoracolumbar and caudal vertebrae; increases in the number of sacral vertebrae; increases in the relative length of the neck; decreases in the relative length of the lumbar portion of the spine and approximations between thorax and

pelvis; greatly increased stoutness of the trunk in general; marked increases in the widths of the shoulders, chest and hips, extensive lengthening of the lower and, particularly, the upper limb; lengthening of hand and thumb in relation to general body size; increases in relative size of head and in volume of brain (considering general body size); an enormous widening of the sternum; very large increases in the breadth of the ilium, particularly the iliac fossa; and lengthening of the tarsus. This list of phylogenetic trends common to all higher primates could easily be prolonged enormously by enumerating the findings of other investigators in the many special fields of science not even mentioned in this paper. The above random examples suffice to support the general deduction that the group of higher primates could not be characterized by manifestations of so many identical trends, if they had not been endowed with these same tendencies from one common ancestral source. Unquestionably, some of the above named and many additional common trends of higher primates are directly or indirectly connected with the gradual acquisition of the semierect and erect posture, as has been demonstrated by many authors (e.g., Knauer, 1916; Ruge, 1918; Keith, 1923; Morton, 1926; and Gregory, 1928), who have also shown that with the perfection of erect posture such trends have become most pronounced in man, producing many of the extreme conditions which appear as human peculiarities (e.g., Böker, 1935). It is very significant, however, that there also exist a great many common trends among higher primates for which neither the direction of the body axis nor the habit of brachiation can be held responsible. Thus, neither of these factors can by any reasonable argument be connected with the prolongation of the periods of growth or the comparative increase in the size

of the brain, those highly important acquisitions of all higher primates. It also appears most probable that the remarkable plasticity of higher primates was a cause, rather than a consequence, of the development of the upright position.

It remains to consider the much contested problem of the phylogenetic relationships between the various higher primates and, especially, of the relation between man and the anthropoid apes.

Huxley (1864) had already dealt with this problem, reaching the classic conclusion: "that the structural differences which separate Man from the Gorilla and the Chimpanzee are not so great as those which separate the Gorilla from the lower apes" (= lower primates). He specifically added that the differences between man and even the highest apes "are great and significant" and that "the structural differences between Man and the Man-like apes certainly justify our regarding him as constituting a family apart from them." Weinert (1932), on the other hand, places man and the three great apes in one single family containing three genera: one for the orang-utan, one for both African apes, and one for man, the latter two genera representing the single group "*Summo-primates*." The evidence collected in this paper forces the author to agree essentially with Huxley and to disagree radically with the genetic implication of Weinert's classification (most clearly shown in his diagram of the primate family tree) that man and the chimpanzee are much more closely related than the chimpanzee and the orang-utan. That the latter conclusion is untenable has most recently also been shown by Straus (1936), who concludes from his comprehensive survey of the thoracic and abdominal viscera of primates that: "Each of the four apes and man exhibits a definite mosaic of visceral characters, some rather primitive, some

intermediate, and some highly specialized. There is nothing in this survey to indicate that man possesses any peculiarly close affinities with the chimpanzee, . . . or even with the chimpanzee-gorilla stock. . . . It might be claimed quite as logically, that man is most closely related to the gibbons."

According to Table 7 man resembles most closely one or the other species of gorillas in 23 out of 57 characters considered, in 15 other characters he is most similar to gibbons or siamangs, and in only the remaining 19 characters does man

be arranged according to their general resemblance, namely: man—gorillas—chimpanzee—orang-utan—*Hylobatidae*. They indicate also that the two African apes stand particularly close together. The latter conclusion is already so well established that it requires no further discussion; indeed, some writings of the past would rather make it appear necessary to emphasize that the differences between chimpanzee and gorilla are sufficiently large to justify their generic separation. It certainly is not to be doubted any more that the gorillas and chimpanzees became

TABLE 7  
*Numbers of characters of closest resemblance among higher primates*

NUMBER OF CHARACTERS regarding which	MAN	GORILLAS	CHIMPAN- ZEE	ORANG- UTAN	HYLO- BATIDAE
<i>Man</i> resembles most closely.....	(57)	23	12	7	15
<i>Gorillas</i> resemble most closely.....	13	(57)	30	12	2
<i>Chimpanzee</i> resembles most closely.....	4	28	(57)	15	10
<i>Orang-utan</i> resembles most closely.....	5	16	19	(57)	17
<i>Hylobatidae</i> resemble most closely.....	11	8	15	23	(57)
Number of Characters showing <i>highest degrees of</i> <i>specialization</i> (Total = 82).....	27	17	6	16	16

The numbers of the characters listed in Table 6 in regard to which any particular type of higher primate resembles most closely the other higher primates and the numbers of characters showing the highest degrees of specialization (including divergent ones) in the various types. Since some characters differ but little in the various types these figures can indicate merely the approximate, average conditions.

resemble most closely either the chimpanzee or the orang-utan. The gorillas differ least from the chimpanzee in regard to 30 of these characters and least from the orang-utan in regard to 12 other characters. According to still other data in the same table the chimpanzee approaches most frequently the gorillas and next frequently the orang-utan, and the latter stands closest to the chimpanzee and about equally close to the *Hylobatidae* and the gorillas. The gibbons and siamangs, finally, are least different from the orang-utan. These figures show chiefly the order in which the higher primates must

phylogenetically divided *after* an independent branch for the orang-utan had appeared. That even the orang-utan diverged from an ancestral stock, common to the great apes, *after* the separation of an evolutionary branch for man, is the only admissible conclusion from the result, to be discussed below, that the general, average differences between the three great apes are smaller and less significant than those between any of the latter and man.

The following characters are peculiar to man and differ at least in the degree of specialization from all the great apes: in all probability the greatest increase in

the duration of postnatal growth; the greatest weight at birth in relation to body weight in adult life; the largest relative brain size; complete bipedal walk and erect posture; greatest reduction in density of hair (except on scalp) and occurrence of wavy and curly hair; universal absence of ischial callosities; probably earliest disappearance of an independent *os centrale*; rarity and lateness of fusion of nasal bones; by far the earliest obliteration of the facial sutures between maxillary and premaxillary bones; by far the latest closure of the great fontanelle; complete lack of penis bone; presence of *ossicula mentalia*, of a true inguinal ligament, and of a transverse metatarsal ligament between toes I and II; unique structure of kidney; highest total number of vertebrae; highest average numbers of thoracolumbar and coccygeal vertebrae; longest cervical and lumbar regions of the spine; the least approximation between thorax and pelvis; least increase in average stoutness of trunk; by far the lowest shoulders; lowest placed nipples; greatest average relative length of lower limbs and shortest average relative length of upper limbs; by far the lowest intermembral index; by far the longest thumb in proportion to the length of the hand and the relatively longest free portion of the thumb; straightness of fingers with extension of palm; by far the shortest relative length of the phalangeal portions of the toes II to V; complete and permanent adduction of hallux; the shortest height of the face in relation to trunk height and, particularly, to size of brain part of head; by far the shortest height of the pelvis, particularly the ilium, in relation to the trunk height and the ilium breadth; the great enlargement of the sacral surface of the ilium; the unique position of the pelvis in regard to the longitudinal axis of the trunk; the unique direction of the *fossa iliaca*; the equality of the sexes in regard

to the size of the canine teeth. This, of course, is a very incomplete list, but it is sufficiently large to support the general claim that a majority of characters separate man more from the great apes than the latter are separated from one another. This general rule is not invalidated by its exceptions, since such exceptions are to be expected with the assumption of a common ancestry for man and all great apes from which they received the same initial characters, among which some can have become modified with exceptional intensity in only one or another type. Genetic relationships can never be reconstructed on the basis of isolated characters alone, but must rest upon the consideration of the more numerous and the more diverse characters the better. The facts that man and the African apes are closely alike in regard to their frontal sinuses (Weinert), their facial muscles (Huber, 1931), etc. are readily explained as instances of parallelism which, according to Clark (1936), are more common in primates than is usually assumed, and they are more than counterbalanced for phylogenetic deductions by the findings that man stands apart from all great apes, while the latter are in most instances closely alike, in regard to the long list of characters already given and in regard to a great many additional features appertaining to the fields of morphology, physiology and psychology. It must also be emphasized here that it is above all the unique combination between many primitive and many other, highly specialized characters which distinguishes man from the great apes. In the latter the typical combinations of the generic variations in the different features are much more similar and uniform than in Weinert's "*Summoprimates*"—man, chimpanzee and gorilla.

Among the characters listed in Table 6 there are 27 in regard to which man is

either most highly specialized or else represents the extreme of a divergent evolutionary trend. The corresponding fig-

the characters discussed here man is twice, as frequently less specialized than one or another anthropoid ape, as he is more spe-

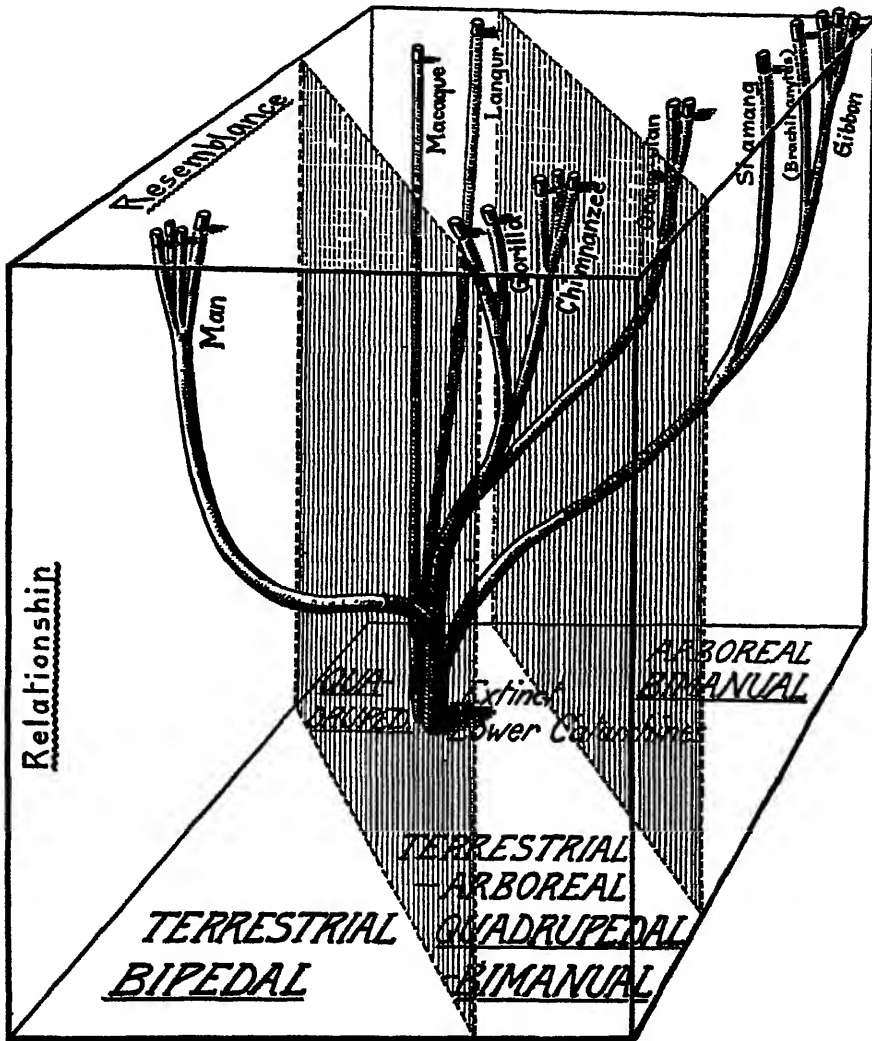


FIG. 21. HYPOTHETICAL, THREE-DIMENSIONAL PEDIGREE OF THE RECENT CATARRHINE PRIMATES AS SUPPORTED BY THE RESULTS OF THIS PAPER AND BY FORMER STUDIES OF THE AUTHOR.

The macaque represents the subfamily *Cercopithecoidea* and the langur the subfamily *Simiinae*. The different habitats and modes of locomotion (underlined) are inscribed on the bottom square.

ures for the anthropoid apes are much smaller, being least of all in the chimpanzee (see Table 7). The latter figures total 55. It can be stated, therefore, that in

cialized, yet he possesses many more extreme specializations than any one of the apes.

The many and profound similarities be-



tween the *Hylobatidae* and the other higher primates, especially the great apes, as well as the numerous peculiarities of gibbons and siamangs have already been discussed in a special paper by the author (1933a) so that only the general deduction needs to be mentioned here, i.e., the *Hylobatidae* branched from the ancestral stock of all higher primates before any of the great apes became separated. This is a well substantiated and quite generally held view. That the *Hominidae*, like the *Hylobatidae*, began to develop as an independent evolutionary branch *before* even the orang-utan had diverged from the common stem of the great apes and that the branch for the former appeared at approximately the same time as, or only slightly later than that for the latter, represents in the

writer's opinion the only theory which can readily account for all the facts known today. From the available evidence it does not seem necessary to separate the phylogenetic branch for man from the stem of the anthropoid apes *before* even the gibbons had become divided from the great apes, as has been done, e.g., in the family tree by Allen and Coolidge (published by Coolidge, 1934). The *Hylobatidae* and man have evolved in opposite directions from a common, early stock, yet in a number of important features they have retained a closer similarity than exists in regard to the same features between man and the great apes.

Figure 21 shows graphically the author's conclusions concerning man's place on the family tree of Old World primates.

#### LITERATURE CITED

- ANKEL, O. 1934. Das Verwandtschaftsverhältnis zwischen dem Menschen und den höheren fossilen Primaten. *Zeitschr. f. Morphol. u. Anthropol.*, 34, 1-14.
- ARLEY-MONTAGU, F. 1935. The premaxilla in the primates. *QUART. REV. BIOL.*, 10, 31-59, 181-208.
- AULMANN, G. 1932. Geglückte Nachzucht eines Orang-utan im Düsseldorfer Zoo. *Zoolog. Garten*, 5, 81-90.
- BÖCKER, H. 1935. Einführung in die vergleichende biologische Anatomie der Wirbeltiere. 1. Bd., *Jena*.
- BOLZ, L. 1926. Vergleichende Untersuchungen an einem Fetus eines Gorillas und eines Schimpansen. *Zeitschr. f. Anat. u. Entwicklungsgesch.*, 81, 1-89.
- BOLTZE, P. 1926. Beiträge zur Anatomie des Knochengerüsts von *Hylobates syndactylus*. *Morphol. Jahrb.*, 56, 317-401.
- BRANDIS, G. 1930. Wichtige Daten über das Heranwachsen des Gorilla. *Zoolog. Garten*, 3, 104-116.
- BROOM, R. 1930. The Origin of the Human Skeleton. *London*.
- CLARK, W. E. LE GROS. 1934. Early Forerunners of Man. A Morphological Study of the Evolutionary Origin of the Primates. *London*.
- . 1935. Man's place among the primates. *Man*, 35, 1-6.
- . 1936. Evolutionary parallelism and human phylogeny. *Man*, 36, 4-8.
- CONNOLLY, C. J. 1932. Brain indices of anthropoid apes. *Amer. J. Phys. Anthropol.*, 17, 57-69.
- COOLIDGE, H. J., JR. 1933. *Pan paniscus*. Pygmy chimpanzee from south of the Congo river. *Amer. J. Phys. Anthropol.*, 18, 1-59.
- . 1934. Our mammalian family tree. *Harvard Alumni Bull.*, 36, 578-580.
- CUNNINGHAM, D. J. 1908. The evolution of the eyebrow region of the forehead with special reference to the excessive supraorbital development in the Neanderthal race. *Transact. Roy. Soc. Edinburgh*, 46, 2, 283-311.
- DUBOIS, E. 1914. Die gesetzmässige Beziehung von Gehirnmasse zu Körpergrösse bei den Wirbeltieren. *Zeitschr. f. Morphol. u. Anthropol.*, 18, 323-350.
- ELFTMAN, H. AND J. MANTER. 1935. The evolution of the human foot, with especial reference to the joints. *J. of Anat.*, 70, 56-67.
- ELLIOT, D. G. 1913. A Review of the Primates. Monograph I, *Amer. Mus. Nat. Hist., New York*.
- FICK, R. 1895. Beobachtungen an einem zweiten erwachsenen Orang-Utan und einem Schimpansen. *Arch. f. Anat. u. Physiol., Anatom. Abh.*, 289-318.
- FISCHER, B. 1933. Genetik und Stammesgeschichte der menschlichen Wirbelsäule. *Biolog. Zentralbl.*, 53, 203-220.
- FOLKE, J. P. 1934. First year development of a Rhesus monkey (*Macaca mulatta*) reared in isolation. *J. of Genetic Psychol.*, 45, 39-105.

- FORSTER, A. 1933/34. Considérations sur l'os central du carpe dans l'espèce humaine. *Arch. d'Anat., d'Histol. et d'Embryol.*, 17, 85-98.
- FRIEDENTHAL, H. 1908. Das Wollhaarkleid des Menschen. Beiträge z. Naturgesch. d. Menschen, I, Jena.
- FULTON, J. F. AND A. D. KELLER. 1932. The Sign of Babinski. A Study of the Evolution of Cortical Dominance in Primates. *Springfield, Ill.*
- GIEBEL, C. G. 1879. Säugethiere. *Bronn's Klassen und Ordnungen des Thier-Reichs*, 6, Abth. 5, Liefer. 23-25.
- GIEBELER, W. 1936. Abstammungskunde des Menschen. *Schriften d. D. Naturkundevereins*, 56, Oebingen.
- GREGORY, W. K. 1927. How near is the relationship of man to the chimpanzee-gorilla stock? *Quart. Rev. Biol.*, 2, 549-560.
- . 1928. The upright posture of man: a review of its origin and evolution. *Proceed. Amer. Philos. Soc.*, 67, 339-376.
- . 1934. Man's Place Among the Anthropoids. *Oxford*.
- . 1935. The pelvis from fish to man: a study in palcomorphology. *Amer. Naturalist*, 69, 193-210.
- HARTMAN, C. G. 1932. Studies in the reproduction of the monkey *Macacus (Pithecus) rhesus*, with special reference to menstruation and pregnancy. *Contrib. to Embryol.*, 23, *Carnegie Inst. Wash. Pub.*, 433; 1-162.
- HARTMANN, R. 1883. Die menschenähnlichen Affen. *Leipzig*.
- HADLÍČKA, A. 1928. Children running on all fours. *Amer. J. Phys. Anthropol.*, 11, 149-178.
- . 1931. Children Who Run on All Fours; and Other Animal-like Manifestations in the Human Child. *New York*.
- HUBER, E. 1931. Evolution of Facial Musculature and Facial Expression. *Baltimore*.
- HUXLEY, T. H. 1864. Evidence as to Man's Place in Nature. *London*.
- JACOB, P. 1899. Ueber Penisknöchel. Inaug.-Dissert., *Univ. Leipzig*.
- JACOBSEN, C. F., M. M. JACOBSEN AND J. G. YOSHIOKA. 1932. Development of an infant chimpanzee during her first year. *Compar. Psychol. Monogr.*, 9, 1-94.
- JONES, F. WOOD. 1929. Man's Place Among the Mammals. *London*.
- KRETZ, A. 1923. Man's posture: its evolution and disorders. *Brit. Med. J.*, 457, 499, 545, 587, 624, 669.
- . 1931. New Discoveries Relating to the Antiquity of Man. *New York*.
- KRETZ, A. 1934. The Construction of Man's Family Tree. Forum Series No. 18. *London*.
- KLEINSCHMIDT, O. 1933. Ueber Stirnbeinhöhlen und Siebbeinzellen beim Orang. *Zeitschr. f. Säugetierk.*, 8, 70-71.
- KNAUER, S. 1916. Ursachen und Folgen des aufrechten Ganges des Menschen. *Anatom. Hefte*, II. Abt., Ergebnisse, 22, 1-155.
- LEBOUCQ, H. 1884. Recherches sur la morphologie du carpe chez les mammifères. *Arch. de Biol.*, 5, 35-102.
- LÖNNBERG, E. 1917. Mammals collected in Central Africa by Captain E. Arrhenius. *Kungl. Svenska Vetenskapsakad. Handl.*, 58, 1-110.
- LORENZ V. LIEBENAU, L. 1917. Beitrag zur Kenntnis der Affen und Halbaffen von Zentralafrika. *Ann. d. k. k. Naturhist. Hofmuseums, Wien*, 31, 169-241.
- LUCAS, J. C. G. 1865. Die Hand und der Fuss. *Abb. Senckenburg. Naturf. Ges.*, 5, 275.
- MAURER, F. 1928. Der Mensch und seine Ahnen. *Berlin*.
- MIDLO, C. 1934. Form of hand and foot in primates. *Amer. J. Phys. Anthropol.*, 19, 337-389.
- MILNE-EDWARDS, A., J. DENIKER, R. BOULART, E. DE POURQUEUR, AND F. DEBILLY. 1895. Observations sur deux orang-outans adultes morts à Paris. *Nouv. Arch. du Mus. d'Hist. Nat.*, 3<sup>e</sup> Sér., 7, 29-118.
- MOLLESON, T. 1933. Phylogenie des Menschen. *Handb. d. Vergleichungswissenschaft.*, 3, *Berlin*.
- MORTON, D. J. 1926. Evolution of man's erect posture. *J. Morphol. & Physiol.*, 43, 147-179.
- . 1927. Human origin. Correlation of previous studies of primate feet and posture with other morphological evidence. *Amer. J. Phys. Anthropol.*, 10, 173-203.
- NOBACK, C. V. 1930. Digital epiphyses and carpal bones in the growing infant female gorilla with sitting height, weight and estimated age. *Zoologica, Scientific Contrib.*, N. Y. *Zoolog. Soc.*, 11, 117-151.
- NOBACK, C. V. 1936. (1) Note on menstruation in the gorilla. (2) Note on gross changes observed in the external genitalia of the female gorilla just before, during and after menstruation. (Abstract.) *Amer. J. Phys. Anthropol.*, 21, Supplem., 9.
- OGILVIE, A. W. 1923. Breeding of the gibbon in captivity. *J. Nat. Hist. Soc. of Siam*, 6, 137.
- OFFENHEIM, S. 1921. Zur Typologie des Primatenkraniums. *Zeitschr. f. Morphol. u. Anthropol.*, 14, 1-203.
- OSBORN, H. F. 1927. Man Rises to Parnassus. Critical Epochs in the Prehistory of Man. *Princeton Univ. Press*.

- OSBORN, H. F. 1930. The discovery of Tertiary man. *Science*, 71, 1-7.
- PUTZNER, W. 1895. Beiträge zur Kenntnis des menschlichen Extremitätenskelets. 3te Abth.: Die Varietäten. *Morphol. Arbeiten*, 4, 347-570.
- PILGRIM, G. E. 1915. New Siwalik primates and their bearing on the question of the evolution of man and the Anthropoidea. *Rec. Geol. Surv. India*, 45, 1-74.
- POHL, L. 1928. Zur Morphologie der männlichen Kopulationsorgane der Säugetiere; insbesondere der Versuch einer vergleichend-anatomischen Studie über den Penis der Primaten, einschliesslich des Menschen. *Zeitschr. f. Anat. u. Entwicklungsgesch.*, 86, 71-119.
- POUSARGUES, E. DE. 1895. Note sur l'appareil génital male des orang-outans. *Novv. Arch. du Mus. d'Hist. Nat.*, 3<sup>e</sup> Sér., 7, 57-82.
- RAVEN, H. C. 1936. Genital swelling in a female gorilla. *J. of Mammalogy*, 17, No. 4.
- REICHENOW, E. 1921. Contribucion a la biologia de los antropomorfos africanos. *Real Soc. Espanola de Hist. Nat.*, T. Extraordin., 337-348.
- REYNOLDS, E. 1931. The evolution of the human pelvis in relation to the mechanics of the erect posture. *Papers of Peabody Mus. of Amer. Archaeol. & Ethnol.*, Harvard Univ., 11, 249-334.
- RICHTER, C. P. 1931. The grasping reflex in the new-born monkey. *Arch. Neurol. & Psych.*, 26, 784-790.
- ROMANES, G. J. 1892. Darwin, and After Darwin. I. The Darwinian Theory. *London*.
- RUOZ, G. 1918. Die Körperformen des Menschen in ihrer gegenseitigen Abhängigkeit und ihrem Bedingsein durch den aufrechten Gang. *Leipzig*.
- SCHAEFFER, J. P. 1920. The Nose, Paranasal Sinuses, Nasolacrimal Passage-ways, and Olfactory Organ in Man. *Philadelphia*.
- SCHULTZ, A. H. 1926. Fetal growth of man and other primates. *QUART. REV. BIOL.*, 1, 465-521.
- . 1927. Studies on the growth of gorilla and of other higher primates with special reference to a fetus of gorilla, preserved in the Carnegie Museum. *Memoirs, Carnegie Mus.*, 11, 1-88.
- . 1929. The technique of measuring the outer body of human fetuses and of primates in general. *Contribut. to Embryol.*, 20, *Carnegie Inst. Wash. Pub.* 394, 213-257.
- . 1930, a. The skeleton of the trunk and limbs of higher primates. *Human Biol.*, 2, 303-438.
- . 1930, b. Notes on the growth of anthropoid apes with especial reference to deciduous dentition. Report, Labor. & Mus. Comp. Pathol., Zoolog. Soc. *Philadelphia*, 34-45.
- . 1931, a. The density of hair in primates. *Human Biol.*, 3, 303-321.
- SCHULTZ, A. H. 1931, b. Man as a primate. *Scientific Monthly*, 33, 385-412.
- . 1933, a. Observations on the growth, classification and evolutionary specialization of gibbons and siamangs. *Human Biol.*, 5, 212-255; 385-428.
- . 1933, b. Die Körperproportionen der erwachsenen catarrhinen Primaten, mit spezieller Berücksichtigung der Menschenaffen. *Anthropolog. Anz.*, 10, 154-185.
- . 1933, c. Chimpanzee fetuses. *Amer. J. Phys. Anthropol.*, 18, 61-79.
- . 1933, d. Notes on the fetus of an orang-utan with some comparative observations. Report, Labor. & Mus. Comp. Pathol., Zoolog. Soc. *Philadelphia*, 28-39.
- . 1933, e. Growth and Development. The Anatomy of the Rhesus Monkey. Edited by Hartman & Straus. *Baltimore*, 10-27.
- . 1934. Some distinguishing characters of the mountain gorilla. *J. of Mammal.*, 15, 51-61.
- . 1935. Eruption and decay of the permanent teeth in primates. *Amer. J. Phys. Anthropol.*, 19, 489-581.
- . 1936. Fetal growth and development of the Rhesus monkey. *Contribut. to Embryol.*, 26, *Carnegie Inst. Wash. Pub.* (in press).
- SCHULTZ, A. H. AND F. F. SYNDER. 1935. Observations on reproduction in the chimpanzee. *Bull. Johns Hopkins Hosp.*, 57, 193-205.
- SCHWABER, G. 1926. Ueber das Intermetatarsium. *Zeitschr. f. Morphol. u. Anthropol.*, 20 1-50.
- . 1923. Die Abstammung des Menschen und die ältesten Menschenformen. Kultur d. Gegenwart, Abt. 5, Anthropologie; *Leipzig*, 223-338.
- SMITH, ELLIOT, G. 1924. The Evolution of Man. Essays. Oxford Univ. Press.
- SOMMER, C. F. 1923. On the pelvic muscles and generative organs in the male chimpanzee. *Proc. Zoolog. Soc. London*, 1001-1011.
- . 1924. The Morphology and Evolution of the Apes and Man. *London*.
- STEGGERDA, M. AND R. MILLAR. 1936. Finger lengths of the Maya Indians as compared with negroes and whites. Measures of men. *Middle Amer. Research Ser., Pub. 7*; Tulane Univ., 83-100.
- STEWART, T. D. 1936. The musculature of the anthropoids: Neck and trunk. *Amer. J. Phys. Anthropol.*, 21, 141-204.
- STRAUS, W. L., JR. 1929. Studies in primate ilia. *Amer. J. Anat.*, 43, 403-460.
- . 1930. The foot musculature of the highland gorilla (*Gorilla beringei*). *QUART. REV. BIOL.*, 5, 261-317.
- . 1934. The structure of the primate kidney. *J. of Anat.*, 69, 93-108.

- STRAUS, W. L., JR. 1936. The thoracic and abdominal viscera of primates, with special reference to the orang-utan. *Proc. Amer. Philos. Soc.*, 76, 1-85.
- TOMILIN, M. I. 1936. Length of gestation period and menstrual cycle in the chimpanzee. *Nature*, 137, 318-319.
- TURNER, L. 1901. The Accessory Sinuses of the Nose. *Edinburg.*
- TYSON, E. 1699. Orang-outang, sive Homo sylvestris: or, the anatomy of a pygmy compared with that of a monkey, an ape, and a man. *London.*
- VIRCHOW, H. 1917. Ueber Fussskelette farbiger Rassen. *Berlin.*
- . 1929. Das Os centrale carpi des Menschen. *Morphol. Jahrb.*, 63, 480-530.
- WATERMAN, H. C. 1929. Studies on the evolution of the pelvis of man and other primates. *Bull. Amer. Mus. Nat. Hist.*, 58, 585-642.
- WEBER, M. 1928. Die Säugetiere, II. Systematischer Teil. *Jena.*
- WEIDENREICH, F. 1921. Der Menschenfuss. *Zeitschr. f. Morphol. u. Anthropol.*, 22, 51-282.
- . 1931. Der primäre Greifcharakter der menschlichen Hände und Füße und seine Bedeutung für das Abstammungsproblem. *Verhandl. Ges. f. Phys. Anthropol.*, 97-110.
- WEINKERT, H. 1926. Die Ausbildung der Stirnhöhlen als stammesgeschichtliches Merkmal. *Zeitschr. f. Morphol. u. Anthropol.*, 25, 243-357, 365-418.
- . 1932. Ursprung der Menschheit. Ueber den engeren Anschluss des Menschengeschlechts an die Menschenaffen. *Stuttgart.*
- WELLS, L. H. 1931. The foot of the South African native. *Amer. J. Phys. Anthropol.*, 15, 185-289.
- . 1935. A peroneus tertius muscle in a chacma baboon. *J. of Anat.*, 69, 508-514.
- WERTH, E. 1921/28. Der fossile Mensch. Grundzüge einer Paläanthropologie. *Berlin.*
- WILDER, B. G. 1862. Contributions to the comparative myology of the chimpanzee. *Barton J. Nat. Hist.*, 7, 352-384.
- WIBLOCKI, G. B. 1932. On the female reproductive tract of the gorilla, with a comparison of that of other primates. *Contrib. to Embryol.*, 23, *Carnegie Inst. Wash. Pub.* 433; 163-204.
- YERKES, R. M. AND A. W. YERKES. 1929. The Great Apes. A Study of Anthropoid Life. *New Haven.*
- ZUCKERMAN, S. 1933. Functional Affinities of Man, Monkeys, and Apes. *New York.*
- ZUCKERMAN, S. AND A. E. SUDERMAN. 1935. Serum relationships within the family Cercopithecidae. *J. of Experim. Biol.*, 12, 221-228.



---



---

## NEW BIOLOGICAL BOOKS

*The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.*

### BRIEF NOTICES

#### EVOLUTION

##### THE VARIATION OF ANIMALS IN NATURE.

By G. C. Robson and O. W. Richards.  
Longmans, Green and Co., New York.  
\$8.25. 8 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; xvi + 425 + 1 plate;  
1936.

In many ways this is an important book. It deals with an interesting subject; evaluates a large group of data critically; points out many gaps and problems yet to be attacked, and generally attests the fact that the authors have more than a reading acquaintance with much of their text discussion. The question of variation of animals in nature is a problem too often overlooked and too often underestimated. The central theme of this book has been to collect facts as to how animals vary and then apply specific evolutionary theories to these facts in an attempt to see which theory or theories best fit the actual material. This is a sound procedure.

The volume is divided into eight chapters headed as follows: Introduction, The origin of variation, The categories of variant individuals, The distribution of variants in nature, Isolation, Correlation (*i.e.*, the hanging together of blocks of characters in evolution), Natural selection, Other theories of evolution, Adaptation, and Conclusions. In the final chapter the authors set forth, in a critical fashion, their deductions about the dynamics of evolution. It is impossible to summarize many of these in so brief a review. Of particular interest, however,

is the following passage about natural selection: (p. 373).

We may, perhaps, claim to have shown that group formation is, in part at least, independent of Natural Selection; that the effect of the environment alone cannot give rise to adaptations; and that Natural Selection cannot be excluded from the possible causes of adaptations, though it is more likely to have produced specialization than the more fundamental processes of organization.

This book, distinctly modern in its ideas and approach, should be read by all biologists interested in the theoretical aspects of their subject. It blends competently the talents of the field naturalist, the experimentalist, the geneticist and the statistician. The volume has a carefully selected bibliography and a good index.



REASON AND REVELATION. *Argument for the Truth of Revealed Religion Based Solely upon the Evidences of Science and Philosophy.*

By Edward McCrady. Wm. B. Eerdmans Publishing Co., Grand Rapids. \$3.00.  
9 x 6; 411; 1936.

With reference to evolution the author holds to the following:

Either Evolution is development by means of energies exclusively immanent in the developing material — *i.e.*, exclusively inherent in the very constitution of matter itself, or it is not. If you deny that it is, you simultaneously admit that non-material influences — *yes, immaterial, metaphysical agencies* have cooperated in bringing about the result. Take whichever horn of the dilemma you please.

Mind and personality are considered as true "emergents," using the following concept of "emergence" (the author is here referring to perception):

*a fusion of the potentials of the antecedent mental experiences, and because such integrations are, self-evidently, the very reverse of differentiations or evolutions—involving the formation of new integrals rather than the 'unfolding' (i.e. 'evolution'), actualization or differentiation of the potentials inherent in an already existent integral; and because (in the very nature of things) no mere continuation of a process of pure differentiation can ever in any finite time, result in a process of integration or any process of continued unfolding (evolution) result in a process of enfolding (involution), it is perfectly clear that such integrations and their products, are not the results of Evolution at all, but of external agencies—i.e., agencies foreign to the evolutionary process, and operating in a manner directly opposite to that in which the inherent energies involved in the respective antecedent evolutions are seen to operate.*

The author possesses an extensive acquaintance with the literature of the biological sciences, and manages to use it with considerable acuteness.

It is of interest to note that the second chapter opens with the following lines: "Bitterly hostile to Christianity, impatient of criticism, and undoubtedly given to exaggeration Haeckel is, nevertheless, one of the most original, philosophical, and interesting of all the biologists. The author frankly admits that of all writers on Evolution, Haeckel and Huxley are to him the most fascinating."

For the benefit of the pious we would like to point out that the Rt. Rev. Theo. Bratton, Bishop of Mississippi, thinks very highly of the book.



#### THE EMERGENCE OF HUMAN CULTURE.

*By Carl J. Warden. The Macmillan Co., New York. \$2.00. 7½ x 5½; x + 189; 1936.* The author has a great deal to say about the meaning of culture, the biosocial status of animals (social insects, birds and higher mammals), the evolution of culture, and culture and progress. In the section on the emergence of human culture he analyzes the manifold conditions under which man and culture finally emerge, giving a "brief description of the structural and biosocial characteristics of the

anthropoid ancestors of man and the great apes" and discussing the "common heritage of the pro-human and pro-ape stock from this earlier primate level," the "further evolution of the pro-human stock from this generalized anthropoid level onward," and "how man and culture emerge from the biosocial matrix of the advanced pro-human level." Just how all this actually happened, however, nature seems to have artfully concealed from inquisitive man a long time ago. The volume contains a bibliography, and author and subject indices.



#### OBJECTIVE EVOLUTION.

*By Christopher Playdell-Bouverie. Williams and Norgate, London. 7s. 6d. 8½ x 5½; 233; 1936.*

"This work presents a politico-cosmological ideal whose aim is the evolution of the efficiency of psychic reactions to the status of sense," according to the author in his preface. Naturally, he has to analyse every phase of our civilization. The causes of the world depression are shown, how biologists should regard heredity and environment, how sex should be taught in school and anything else you happen to think of. Finally he explains that most of the world's problems can be solved by a "consumer's monetary expansion policy" much like the Alberta Social Credit Plan. The remaining problems, such as education, are solved separately. Surprisingly enough some few passages are well worth reading.



#### ABSTAMMUNGSLEHRE UND DARWINISMUS. Siebente Auflage.

*By Richard Hesse. B. G. Teubner, Leipzig. 4.20 marks (Germany); 3.15 marks (outside Germany). 9 x 6½; iv + 108; 1936.*

This little book, the outgrowth of six popular lectures delivered by the author in 1901 on the theory of evolution and natural selection, is now in its seventh edition and still maintains its popularity. Its aim is to make evolution clear to the

layman. The volume is well illustrated and brought up to date with respect to recent thought on inheritance.



### GENETICS

METHODIK DER MEDIZINISCHEN ERBFORSCHUNG. *Unter besonderer Berücksichtigung der Psychiatrie.*

By Bruno Schulz. Georg Thieme, Leipzig. M. 10.50 (paper); M. 12 (cloth). 10 x 6½; 189, 1936.

This book on statistical methods as applied to problems of the inheritance of diseases is addressed particularly to workers in the field who feel shy toward mathematics. Therefore it is written in a manner easily understood by a person not specially trained in statistical procedure. Throughout the book examples are given to demonstrate both correct and incorrect methods. A commendable feature is that the theory of probability is developed more extensively than in most elementary statistical textbooks.

The arrangement is in four parts. In the introduction the author stresses the importance of the use of statistics in the solving of problems involving hereditary traits. This is followed by a section on the collection of data (including twin series and other types of comparative data), and sources of error. In the third part are discussed practically all of the current methods of working out and deriving conclusions from the data collected, together with methods of testing the correctness and significance of results. The final section discusses genealogical investigations and also contains a summary of the most important points in the book.

The nine-page bibliography contains a short list of textbooks and journals on human and general genetics and a longer documentation of the book, arranged by topics of the individual chapters. There is an index.



LES BASES SCIENTIFIQUES DE L'AMÉLIORATION DES PLANTES (*Biologie—Génétique—*

*Écologie—Biométrie—Statistique*). *Encyclopédie Biologique XIII.*

By F. Boeuf. Paul Lechevalier, Paris. 140 francs. 10 x 6½; iv + 543; 1936 (paper).

This book, primarily devoted to Tunisian needs, is divided into three major parts. The first is devoted to a brief exposition on living matter, cellular structure, and the reproduction and multiplication of plants. The laws of heredity, the principles of evolution, and an exposition of the biomorphological basis of plant systematics constitute the second part. The third part is devoted to the scientific basis of plant amelioration: selection, different ways of plant reproduction, adaptation of plant cultures to different physical and chemical environments and the control of results by using comparable scientific methods are discussed.

On the whole, there are relatively few new scientific facts, since the primary aim of the book is to present in a comprehensive way the scientific basis of modern plant culture.



EL DESARROLLO Y LA RELACIÓN NUMÉRICA ENTRE LOS SEXOS EN LOS HÍBRIDOS INTERESPECÍFICOS OBTENIDOS POR FECUNDACIÓN ARTIFICIAL EN EL GÉNERO *TRITON* (MOLGE).

By Käte Pariser. Museo Nacional de Ciencias Naturales, Madrid. 9½ x 6½; 93 + 1 plate; 1936 (paper).

In this book are given the results of experiments on the development of sexual characters and the sex ratio in the offspring obtained in the natural manner and by artificial fertilization and crossing of the four species of *Triton* indigenous to Germany—namely, *taeniatus*, *palmaris*, *alpestris* and *cristatus*. With the exception of the crosses between *taeniatus* and *palmaris* the offspring from the various combinations of parents were influenced in color and size by the male parent. The *taeniatus-palmaris* and the *palmaris-alpestris* crosses resulted in a 50-50 distribution of males and females in the first generation offspring, whereas with the others the females predominated more and more in successive generations. In some cases only 1.45 per cent of the individuals were

males. A summary in German and a six-page bibliography are provided.



## GENERAL BIOLOGY

**BIOLOGICAL EFFECTS OF RADIATION.** *Mechanism and Measurement of Radiation, Applications in Biology, Photochemical Reactions, Effects of Radiant Energy on Organisms and Organic Products. Volumes I and II.*

Edited by Benjamin M. Duggar, with the Cooperation of Janet H. Clark, Kenneth S. Cole, Farrington Daniels, Gioacchino Failla, Charles Packard and Henry W. Popp. McGraw-Hill Book Co., New York. \$10.00. 9 x 6; xvii + 1343; 1936.

There was a time when the study of light and radiation belonged exclusively in the province of the physicist. Then, at the turn of the century, the biologist entered the picture in a mild way and interested himself primarily with light as a factor in animal behavior. Since that time the field has developed rapidly and today radiation studies from the biological viewpoint represent a lusty department of modern biology and medicine in which many competent investigators are actively engaged. This fact is amply attested by the important two volume book, produced under the auspices of the Committee on Radiation of the National Research Council, here under review. This is a book replete with many authoritative data, theoretical interpretations and extended bibliographies all prepared by experts and dealing with such diverse topics as photons and electrons; measurements of X-rays and radium; ionization and its bearing on biological phenomena; photochemistry; mitogenetic rays; statistical treatment of radiation data; radiation effects on proteins, vitamins, embryonic development, regeneration, protoplasm, behavior of the organism as a whole, various kinds of plants, growth, mutations, bacteria, enzymes, etc., etc. As a whole, the standard of the work is high and the volumes should carve for themselves a long-time niche among scientific reference books. As is inevitable with compendiums of this kind there exists little real correlation between particular sections, and each

chapter actually represents a distinct essay dealing with one phase of radiation phenomena. The book is adequately illustrated, briefly indexed and cites an admirable number of pertinent references.



**L'ŒUF.** *Essai de Théorie de sa Segmentation.*

By G. Monteil. G. Doin and Cie., Paris. 18 francs. 9 x 5½; 68 + 16 plates; 1936 (paper).

This is a study of the geometrical principles underlying the process of segmentation, using as examples, for the most part, the eggs of the amphibians and annelids. The theoretical development is extremely condensed, the numerous diagrams to illustrate it so complicated as to be of not the greatest help, and the subject itself a very abstruse and difficult one. The fundamental bases of the theoretical discussion are (1) that, except for eggs of very unequal segmentation, at the anaphase the asters will reach the centres of gravity of the blastomeres in process of formation, the points at which the nuclei will be found at the telophase. (2) For all phases where segmentation is in parallels of the egg sphere, the axes of the spindles will never be vertical, and the planes of segmentation never horizontal. From these bases a series of consequences are deduced, well worth the consideration of embryologists and those interested in the shape of cells in multicellular organs and tissues. An important but difficult book.



**T. H. HUXLEY'S DIARY OF THE VOYAGE OF H. M. S. RATTLESNAKE.**

Edited from the Unpublished M.S. by Julian Huxley. Doubleday, Doran and Co., Garden City, New York. \$3.00. 9 x 6; xiv + 301 + 13 plates; 1936.

"Not events merely but those which influence a man, are of importance." This line from the recently found manuscript diary of Thomas Henry Huxley is a cue to the spirit in which this journal—a record of four years spent as assistant-surgeon and



naturalist aboard H. M. S. Rattlesnake—was kept. The scientific enterprises of this period which won him his place as fellow in the Royal Society at the age of twenty-five are not treated at great length here, but it is of interest to follow his moods and watch the play of his mind in evaluating himself and his work at this time. It was a period of great turmoil, particularly after he met and fell deeply in love with Henrietta Heathhorn who was to become his wife nine years later. During the fourth voyage the emotional upheaval had somewhat subsided, and here we have interesting accounts of islands visited with vivid word pictures of native life and customs. The book is illustrated with sketches and scientific drawings by Huxley, and a few photographs.



ZEIT-ORDNUNGSFORMEN DES ORGANISCHEN LEBENS. *Bios, Band 5.*

By E. Ungerer. *Johann Ambrosius Barth, Leipzig.* 4.50 marks.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; vi + 72; 1936 (paper).

The author discusses the rôle of time in organic life, beginning with a comparison of aging, death, and reproduction in one-celled and many celled organisms. He then discusses the periodic organization of organic events as the life cycles of many animals and plants, periodic reproduction phases, etc. Less clear and more speculative is the third section on periodic forms of behavior among animals and man. A short section dealing with the comprehension of time and the ability to save time by means of a feeling of an "inner clock," leaves one rather mystified. The author tends to ally himself with the vitalistic philosophers.



SOCIAL BIOLOGY. *A Textbook for Secondary Schools.*

By Everett P. Walton and Philip E. Foss. *P. Blakiston's Son and Co., Philadelphia.* \$1.68.  $7\frac{1}{2} \times 5\frac{1}{2}$ ; xv + 537; 1936.

In our opinion there is not the smallest reason for giving this good, but in no way

extraordinary, high school text book of biology the title *Social Biology*. In fact to do so verges a bit closely upon misrepresentation. The book contains no more, and essentially no different, material about man than do many other secondary school texts in biology at the present time. And perhaps if the authors had read William Morton Wheeler's famous paper *Termitodora* they would not have headed the last section of their book with the words: "Man is the only animal with a social heritage."



ELEMENTS OF GENERAL BIOLOGY.

By Henry R. Barrows. *Farrar and Rinehart, New York.* \$2.60.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; x + 435; 1936.

This volume was practically completed before Dr. Barrows' death last summer. While based on his larger book, it is in no sense an abridgement since much of the purely morphological material is omitted, some of the sections (especially those in chemistry and physics of protoplasm) have been simplified, and many other changes in the handling of the material and illustrations have been made. In a group of appendices are given a brief classification of plants and animals, notes on vitamins, brief biographical skeletons of biologists of the past, a bibliography and a glossary. The volume is indexed.



FOUNDATIONS OF BIOLOGY. *Fifth Edition.*

By Lorando L. Woodruff. *The Macmillan Co., New York.* \$3.50.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; xiv + 583; 1936.

The third and fourth editions of the Foundations of Biology have been mentioned in previous numbers of the Q. R. B. (Vol. 3, No. 1 and Vol. 6, No. 1). The present edition has been thoroughly revised, new material has been added, especially in the field of genetics, and there are many new illustrations. Two additional chapters, give a synoptic view of the plant and animal kingdoms. The view point of the earlier editions has been strictly adhered to—namely, to present a

broad survey of the fundamental principles of biology for the college student and the general reader.



**MANUAL OF BIOLOGY. Fifth Edition.**

By George A. Baitsell. The Macmillan Co., New York. \$2.50. 8½ x 5½; xi + 434; 1936.

In this fifth edition of a well-known laboratory manual a considerable amount of new material has been added, especially in connection with plant types (notably the algae, colorless plants and seed plants). On the animal side, the grasshopper has been added as a type form and the treatment of the vertebrate extended. In many of the chapters a section on *Related facts of importance* has been included for the interest of the more advanced student. The volume contains twelve plates, each chapter is documented and there is an index.



**COMPARAISON ENTRE LA RYTHMICITÉ DES COURANTS D'ACTION CELLULAIRES CHEZ LES VÉGÉTAUX ET CHEZ LES ANIMAUX. Actualités Scientifiques et Industrielles, 314.**

By Daniel Auger. Hermann et Cie, Paris. 20 francs. 10 x 6½; 101; 1936 (paper).

This number of the *Actualités* series is an important contribution in the field of electrophysiology. The author has made an extensive study of the pulsating phenomena of plant tissues, using mainly *Nitella* and *Chara*, and compared their rhythmic behavior to that of animal tissues. Comparison showed that "in spite of the diversity of the rhythms and the variety of origin of the cells on which they were observed, the pulsating systems showed a great unity of behavior."



**DEEP SEAS AND LONELY SHORES.**

By W. Lavallin Puxley. E. P. Dutton and Co., New York. \$2.50. 8 x 5½; 215 + 4 plates; 1936.

A wealth of information is contained in this interesting book. The author has

wandered extensively all over the world and he writes for the general reader, who is especially interested in natural history and popular science, of what he has observed concerning the many beautiful and weird creatures that inhabit the seas in many out of the way places. Four illustrations are included in the volume but there is no index.



**COLLEGE BIOLOGY.**

By Walter H. Wellbouse and George O. Hendrickson. F. S. Crofts and Co., New York. \$3.00. 8½ x 5½; viii + 381; 1936.

This is a textbook designed more for "the general student" than for the future biologist, and as such, is fairly well composed. However, we do not feel that thirteen pages of generalized discussion is enough to devote to the entire Phylum Arthropoda in a college course in biology. The bibliography is poor.



**ATMOSPHERIC POLLUTION OF AMERICAN CITIES FOR THE YEARS 1931 TO 1933 with Special Reference to the Solid Constituents of the Pollution. U. S. Treasury Department. Public Health Service. Bulletin No. 224.**

By James E. Ives, Rollo H. Britten, David W. Armstrong, W. A. Gill and Frederick H. Goldman. United States Government Printing Office, Washington. 10 cents. 9½ x 6½; iv + 75 + 1 plate; 1936 (paper).

This study indicates that atmospheric pollution is greater in winter, on weekdays, and when the wind velocity is low. There is great variation at different times of day but "aside from the morning maximum, the density of the pollution during the day appears to depend largely on the vertical air currents." Rain does not cause a decrease in atmospheric pollution. A useful volume for the ecologist to have on his shelf.



**FLOODS IN THE UNITED STATES. Magnitude and Frequency. U. S. Department of the**

*Interior, Geological Survey. Water-Supply Paper 771.*

By Clarence S. Jarvis and Others. Prepared in collaboration with the Water Planning Committee of the National Resources Board and its predecessor the Mississippi Valley Committee. U. S. Government Printing Office, Washington. \$1.00. 9 $\frac{1}{8}$  x 5 $\frac{1}{8}$ ; 497 + 3 folding plates; 1936 (paper).

Numerous tables are given concerning the flood peaks and other flow characteristics of flood rises for the various river basins both in the eastern and western parts of the United States. The data are subjected to an extended statistical analysis. Again a useful treatise for the ecologist.



## HUMAN BIOLOGY

CORAL GARDENS AND THEIR MAGIC. *A Study of the Methods of Tilling the Soil and of Agricultural Rites in the Trobriand Islands. Volume 1, The Description of Gardening; Volume 2, The Language of Magic and Gardening.*

By Bronislaw Malinowski. American Book Company, New York. \$8.00 per set. 9 $\frac{1}{2}$  x 6; Vol. 1, xxxv + 500 + 69 plates + two folding maps; Vol. 2, xxxii + 350; 1935.

Malinowski says that this book "is the best I have produced or am ever likely to produce." It certainly is a masterpiece, and, if he feels that way about it, it may well stand as the crowning work of a great anthropologist—in fact now one of the world's foremost.

The first volume is analytically descriptive of the objective phenomena of Trobriand agriculture. The second volume divides itself between the setting forth of an ethnographical theory of language, and a *Corpus Inscriptum* that is the whole work's basic documentation.

In the space available we cannot convey to the reader the scope and meaning of the book any better or more concisely than in Malinowski's own words.

In this book we are going to meet the essential Trobriander. Whatever he might appear to others, to himself he is first and foremost a gardener. His passion for his soil is that of a real peasant. He experiences a mysterious joy in delving into the earth, in turning it up, planting the seed, watching the

plant grow, mature, and yield the desired harvest. If you want to know him, you must meet him in his yam gardens, among his palm groves or on his taro fields. You must see him digging his black or brown soil among the white outcrops of dead coral and building the fence, which surrounds his garden with a "magical wall" of prismatic structures and triangular supports. You must follow him when, in the cool of the day, he watches the seed rise and develop within the precincts of the "magical wall", which at first gleams like gold among the green of the new growth and then shows bronzed or grey under the rich garlands of yam foliage.

The side of tribal life described in these volumes is perhaps less sensational than the sailing and trading and witchcraft known to the readers of the *Argonauts of the Western Pacific*; it may have less direct appeal to our curiosity than the customs of courtship and marriage treated in *The Sexual Life of Savages*. But it is at least as important for our knowledge of the Trobrianders, of Oceanic civilisations and, I venture to say, even of human nature in general.

For, on the one hand, nothing bears so directly on man's economic nature as the study of primitive forms of tilling the soil. The manner in which so-called savages produce their primary sustenance, store it and handle it, the way in which they surround it with magical and religious beliefs, open problems of the relation between man and environment of some importance to economic philosophy. On the other hand, agriculture and its consequences enter very deeply into the social organisation of our South Sea community—and of any community for that matter; they form the foundation of political power and of domestic arrangements; they are the mainstay of the obligations of kinship and of the law of marriage. Thus in many ways the perusal of the present book may add to our knowledge of primitive economic organisation, political order, and domestic life.



THE RELATION BETWEEN MORALITY AND INTELLECT. *A Compendium of Evidence Contributed by Psychology, Criminology, and Sociology.*

By Clara F. Gaskell. Teachers College, Columbia University, New York. \$4.50. 9 x 6; xviii + 556 + 1 folding chart; 1936.

This volume represents an investigation covering many years of work. It incorporates the material of a dissertation presented in 1920 (entirely rewritten), includes additional data, and introduces certain refinements in the presentation and in the statistical treatment. Many important studies published since the original thesis appeared have been included in the study. These have been subjected to a "uniform tabular method of report, synthesized and merged in a compilation of the correlational results of the research

as a whole." The general subjects dealt with include delinquency and mental inferiority, moral character and intelligence, moral and intellectual traits, conduct and intelligence and a consideration of factors which effect results.

The author finds that

The relation between morality and intellect in restricted groups is clearly direct. The obtained relation is extremely variable, but tends to be low. The true relation is undoubtedly higher than the obtained relation, but apparently at best it tends to be only marked and frequently it tends to be low. Expressed in correlational terms, the obtained relation may therefore usually be expected to fall between .10 and .39, and the true relation to be under .50." It is believed that "Undoubtedly the relation between morality and intellect in the general population is considerably higher than that usually found in restricted groups. Nevertheless, it is hardly probable that this relation is high. Expressed in correlational terms, the relation in the general population may therefore be expected to fall below .70.

Much tabular material is included in the text and a good deal of supplementary material is added in four appendices. There is a bibliography of 214 titles and an author and a subject index.



THE HERITAGE OF THE BOUNTY. *The Story of Pitcairn Through Six Generations.*

By Harry L. Shapiro. Simon and Schuster, New York. \$3.00. 9 x 5½; xv + 329; 1936.

The mutiny on the Bounty started no differently than many another difference of opinion between masters and men aboard ship, but in the end it produced the world's tidiciest and most interesting experiment in human biology to date. Thanks to the painstaking research and literary skill of Messrs. Nordhoff and Hall everyone just now knows the main features of the story of Pitcairn Island. Dr. Shapiro caps the climax by going to Pitcairn and studying the present-day descendants of the mutineers, with all the refined technique of the modern physical and social anthropologist. An experiment in human race crossing has been as adequately dealt with as is possible under all the circumstances.

The present volume is a popular account of Dr. Shapiro's experiences and some of

the results. More technical reports will appear elsewhere later. He has done an excellent job in this book. His literary skill charms and fascinates as well as informs, and his illustrations are superb—so much so that the only pity is that there are not more of them.

Space is lacking to discuss the many points of extraordinary interest brought out in the book. One, however, we must mention; the decline in fertility. The following table gives the facts for all women who lived to 45 and were married up to that age.

Birth Year of Mother	Number of Women	Average Number of Children per Female
1790-1814.....	1	6.0
1815-1839.....	5	11.4
1840-1864.....	8	8.0
1865-1889.....	20	5.0
1890-1914.....	2	2.5

Dr. Shapiro rather leans to the view that venereal disease may have played a significant rôle in this fertility decline. It seems certain that contraception did not, though conceivably it may have had some small part in bringing about the observed result.

The book is well indexed, and we recommend it unreservedly.



THE SQUATTING AGE IN AUSTRALIA 1835-1847.

By Stephen H. Roberts. Melbourne University Press, Melbourne. 218. 8½ x 5½; x + 455; 1936.

Between 1835 and 1847, Australia was transformed from a penal colony to the most important wool producing country in the world. Credit for the transformation is due to the foresight and ability of a few large land-owners and the daring and persistence of the so-called squatters. These were men of all classes and conditions who defied the laws and the opposition of the existing land-owners, went out into the wild country and settled on extensive tracts of forbidden land and raised sheep on a large scale. The author portrays vividly and, at times, with unbecoming passion, the interplay of political, social and economic factors

which centered around the squatting movement. As seen by him, on the one hand there were the authorities in England, mostly theorists with little knowledge of the needs of the colony, who cooperated little with and impeded greatly any intelligent attempt of the local governors to aid the progress of the colony. The governors, on the other hand, were forced to battle the local politicians in the service of the large proprietors who were interested in their own financial well-being. The main point of contention was the question of whether an individual had the right to occupy and keep land that belonged to the Crown. And of course those who had land were for a strict observance of the laws. While the political struggle raged the squatting movement went on. The author brilliantly traces the evolution of the squatter; first a vilified interloper and finally a staunch defender of the *status quo* against the newcomers seeking gold. In the meantime the local governors and the ministry in England blundered along only to be forced, after a number of years, to acquiesce to a state of fact.

While one may not always agree with the author's interpretations, nevertheless he succeeds in showing effectively the futility of laws and pre-determined regulations when they seek to put a limitation to one of the most important human activities, that of making a living; or attempt to stop what was once called social capillarity.



INSTITUTIONAL TREATMENT OF DELINQUENT BOYS. *Part 2. A Study of 751 Boys.* U. S. Department of Labor. *Children's Bureau Publication No. 230.*

By Alida C. Bowler and Ruth S. Bloodgood. U. S. Government Printing Office, Washington. 15 cents.  $9\frac{1}{2} \times 6$ ; v + 149; 1936 (paper).

This is the second part of a report on 751 delinquent boys who were committed for some time to State Institutions in either California, Michigan, New Jersey, New York or Ohio. (The first part of this report was reviewed in Q. R. B. Vol. 10, No. 4, 1935.) Here the authors present

statistical data regarding (a) pre-commitment history of the boys: age, home and environmental conditions, type of offense; (b) institutional treatment: vocational training, conduct, etc.; (c) conduct of the boys on parole and after leaving the institutions. Information regarding this last item is of particular importance because from it one can judge the value of institutional care. It is sad to learn that 77 percent of the boys did not or could not utilize the trade learnt in the institution. Moreover, the majority of the boys about five years after their release from the institutions, were earning very low incomes. In relation to this, the authors note that of 10 percent of the boys earning average incomes or better, a number derived their high income from illegal enterprises. The most significant fact observed in this investigation is that 66 percent of the boys for whom information was available, had been arrested once or more since their release from the institution and that 42 percent had been committed to some penal institution.

While these findings are not altogether new, they demonstrate again that something is definitely wrong with the method by which these sample institutions attempt to educate and reform the children. The authors are aware of this but nevertheless limit themselves to mild ineffectual criticism.



KENYA. *Contrasts and Problems.*

By L. S. B. Leakey. Methuen and Co., London. 7s. 6d.  $7\frac{1}{2} \times 5$ ; xiii + 189 + 8 plates; 1936.

The author, who was born in Kenya and has acquired a considerable knowledge of the country and its peoples from his anthropological studies there, does not see eye to eye with the British administration of this territory. In the first place, he believes that conflict with the natives arises from the fact that the British administrators do not understand the point of view of the natives nor are the local Colonial officials given a chance to learn. In the second place, it is evident that as the education of the natives proceeds they will demand more and more

political rights and this will augment the tension already existing between natives and the white settlers. In the author's opinion, it will be better for the white settlers engaged in agricultural enterprises to return to England and leave the land to the natives. He observes that the physical aspects of the country are changing in a way unfavorable for modern agricultural methods and therefore the white men will suffer while the natives with their "uncivilized" methods can still use the soil to great advantage. Only in the development of the mineral resources will the white man obtain the greatest profit from this country with benefit to England and the natives of Kenya.

The book is engagingly written and contains excellent chapters on the physical aspects of the country and its geologic formations; on the means of traveling; and on the missionary work.



#### BALUBA ET BALUBAÏSES DU KATANGA.

By *Edmond Verbulpen*. *L'Avenir Belge, Anvers*. 150 francs (paper), 180 francs (cloth) in Belgium; 175 francs (paper), 210 francs (cloth) outside of Belgium. 10 x 6½; 534 + viii + 2 folding maps; 1936.

The legends and traditions of the natives constitute the sources from which the author derives this outline of the political history of the Baluba tribes that inhabit the Belgian Congo. Sometime in the 15th century the Balubas invaded this region and established an empire. This history begins from that epoch and the author traces the fortunes of the rulers of the region from that period to the present day. He includes brief notes regarding their achievements, the forms of government, the administrative subdivisions, the titles of the officials and their prerogatives and functions. No one can doubt that obtaining these data was a formidable task. Regarding their accuracy, the author points out that the dates and facts as he notes them are internally consistent as to chronology, and are in agreement with the reports of the early explorers and administrators of this and contiguous

regions. The author himself was at one time administrator of the Belgian Congo, and this book is written in the style of an official report. Very little is mentioned about the ethnology of these peoples, but the author includes a small vocabulary, genealogic charts and excellent maps.

To the human biologist and sociologist, in particular, this book will be welcome especially because of its extensive bibliography on the subject of the Balubas.



#### GEOGRAPHY. *An Introduction to Human Ecology.*

By *C. Langdon White and George T. Renner*. *D. Appleton-Century Co., New York*. \$4.00. 8½ x 6; x + 790 + 1 folding chart; 1936.

An important text book for college and university students which embodies all the important advances that the study of geography has made in recent years. In brief it is a study of man's conquest of the land and water of the earth, of the losses to which the natural resources are being subjected through mismanagement, and of the methods by which these can be conserved. It includes also the economical, social and political reactions of man in different environments. The volume is divided into ten parts. The first deals with human ecology and the geographical elements, then follow sections on the climatic factor (11 chapters); the biotic factors (2 chapters); the physiographic factor (4 chapters); the edaphic factor (2 chapters); the mineral factors (3 chapters); the hydrographic factors (3 chapters); spatial factors (5 chapters); the geographical unit (4 chapters); and the social factor (1 chapter). The volume is generously illustrated with photographic reproductions, charts and maps, and has an excellent working index. The senior author is professor of geography in Western Reserve University and the junior author is senior economist of the U. S. National Resources Committee.



#### THE MEDICAL DICTIONARY AND OTHER BIOGRAPHICAL STUDIES.

By Major Greenwood. *Williams and Norgate, London.* 7s 6d.  $7\frac{1}{2} \times 5\frac{1}{2}$ ; 213 + 6 portraits; 1936.

This volume of essays is not only a notable contribution to medical history but also to *belles lettres*, for Professor Greenwood, the distinguished medical statistician, has literary talents far above those of scientific men generally. The discussion is of seven men, of whom six were more or less important figures in the history of medicine—Galen, John Freind, Peter Mere Latham, William Farr, Pierre Charles Alexandre Louis, and William Osler—while the seventh was Greenwood's great and good friend Arthur William Bacot, an amateur entomologist, who became a professional only in the last few and happiest years of his life, only to meet an untimely end from an accidental laboratory infection with typhus, on which he was working experimentally at the time.

The charm of these essays cannot be conveyed in a review. It can only be got by reading them. We warmly recommend that this be done.



#### REINE UND ANGEWANDTE SOZIOLOGIE.

*Eine Festgabe für Ferdinand Tönnies zu seinem achtzigsten Geburtstage am 26. Juli 1936.*

By Albrecht, Boas, Bohnstedt, Bosse, Brenke, Baron v. Brockdorff, Colm, Günther, Harms, Heberle, Hermsberg, Jahn, Jurkat, Kamelopoulos, Löwith, Mainicke, Nicosi, v. Reichenau, Schmalenbach, Sorley, Sorokin, Steinmetz, Steltenberg, Takata, Thurnwald, Wernicke, v. Wiese, Wilbrandt. Hans Buske, Leipzig. 12.37 marks.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; 403 + 1 plate; 1936 (paper).

This symposium of current sociological thought, was occasioned by the 80th birthday of Ferdinand Tönnies, the eminent German sociologist, to whom it has been presented in token of his contributions to sociology. After an introduction by von Wiese, discussing present day trends in sociology, the material is assembled in five sections. Part I deals in general with the history of sociology; Part II with theoretical sociology, systems and methods, and theories of social structure; Part III with empirical soci-

ology and sociography; and Part IV with race theories and philosophy. Part V contains three articles on the life and works of Tönnies.

The majority of the authors are German professors, but besides these there are contributions from distinguished sociologists of America, England, Norway, Japan, Italy, Greece and Holland. Two of the 28 papers are in English. The rest were either originally written in, or have been translated into German.



#### LES RACES HUMAINES.

By P. Laster and J. Millot. *Armand Colin, Paris.* 10.50 francs (paper), 12 francs (bound).  $6\frac{1}{2} \times 4\frac{1}{2}$ ; 223; 1936 (paper).

The first part of this book, written by the senior author, is concerned with physical anthropology. In it he discusses the physical characters of importance for anthropologic investigations, presents a classification of races and describes the characteristics which differentiate the several racial groups. Included is also a chapter on pre-historic man.

In the second part of the book, dedicated to physiological anthropology, the junior author outlines the results of comparative studies on growth, blood types, basal metabolism, development of nervous system, etc. In the concluding chapter the authors discuss the subject of pure races and racial mixtures. They point with pride to the fact that the French people have always remained aloof from the violent debates on the question of racial superiority which, they emphasize, the German people and the Anglo-Saxons of the United States use for political purposes.

Although the bibliography is far from complete, the student interested in human biology will find this little book very useful because it contains much information accurately and clearly related.



FAMILY BEHAVIOR. *A Study of Human Relations.*

By Bess V. Cunningham. W. B. Saunders Co., Philadelphia. \$2.75.  $7\frac{1}{2} \times 5\frac{1}{2}$ ; 471; 1936.

The purpose of this book is to give the college student a general view of the problems concerned with inter- and intra-familial relations. The author discusses the influence of different social and racial origins on the behavior of the members of the family and of the family with its neighbors, the clash of contrasting individual personalities, the education of children, and so on. In fact, every aspect of family life is here studied, but with varying degree of completeness depending on whether the author had at her disposal, for a particular question, the results of psychological and social investigations. The merit of this book lies just in the thoroughness with which she has surveyed the literature on the subject, the extensive bibliography she presents and her ability to interpret the studies she cites. However, for those topics regarding which there are available few or no facts, the author's discussions become very superficial and somewhat resemble the newspaper columns of a Dorothy Dix or Beatrice Fairfax.



ALIEN AMERICANS. *A Study of Race Relations.*

By B. Schrieke. The Viking Press, New York. \$2.50.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; xi + 207; 1936. This volume analyzes and elucidates the problems of certain alien peoples in the United States. The author, a graduate of the University of Leiden, and with 18 years experience in educational affairs in Dutch East Indies, was invited by the Julius Rosenwald Fund to make the survey. During the year that he devoted to this study he informed himself with considerable thoroughness on the Negro problem in the South, on the situation of the Chinese and Japanese in California, and the Mexicans and Indians in the Southwest. In an appendix he discusses Filipino immigration. The larger part of the book is devoted to the southern Negro, particularly his status from the time of the Civil War up to the present.

The student of American race problems

will find little that is new in these pages. The chief value of the book probably lies in the fact that the general reader has at hand a clear and accurate setting forth of the conflict of races in the South and Southwest. The volume is documented and indexed.



WARNING FROM THE WEST INDIES. *A Tract for Africa and the Empire.*

By W. M. Macmillan. Faber and Faber, London. 8s 6d.  $8 \times 5\frac{1}{2}$ ; 213 + 1 folding map; 1936.

Professor Macmillan's description and analysis of social, economic, and political conditions in the West Indies is exceptionally clear and logical. The problem arises from both the economic and the racial situation, the former, he believes, being the major key to the solution of the latter. Professor Macmillan's personal political philosophy naturally conditions the sort of warning he gives. He believes that the economic prosperity as well as the political and social freedom of the colored peoples of Africa and the West Indies are quite as important as those of the whites. Moreover, he thinks it is up to England to do something about it. The danger is that the colored population will not be able to develop into a strong independent peasantry due to the lack of interest if not positive oppression of the whites; and that, therefore, the whites themselves will eventually fail financially and degenerate culturally. His solution is greater coöperation on a more equal footing to secure more efficient agricultural methods.



MORE PROFIT THAN GOLD.

By Joan Arbuthnot. Charles Scribner's Sons, New York. \$2.50.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; 287 + 12 plates; 1936.

An account of surely one of the most completely cockeyed expeditions in search of gold and diamonds ever heard of. To the back country of British Guiana near the eastern border of Venezuela went a party of four Britons, 10♂ and 3♀, of



whom certainly two, maybe three, and perhaps even four could with substantial accuracy be literally described as "babes in the woods." That they did not all die in the jungle appears on the record to have been nothing short of miraculous. They apparently got no gold to amount to anything (the author is uniformly vague about sordid factual matters of a quantitative nature such as dates, etc.). But they had a lot of adventure.

It is a book that any biologist, general or human, is likely to finish if he starts reading it—perhaps because it is so irritating. Its philosophical outlook is basically that of Leicester Square, soaring in its more spiritual moments to that of Picadilly Circus.



ORIENTAMENTO PROFESSIONALE. *Bollettino d'Informazioni*. Anno 1, N. 1; N. 2.

Edited by Giovanni Scanga. Ministero Dell' Educazione Nazionale, Rome. 9½ x 6½; 27 pages each, 1935 and 1936 (paper).

These are the first two numbers of a new periodical published by the Italian Ministry of National Education. Its purpose is to diffuse information on the topic of educational and vocational guidance. Reviews and abstracts of articles dealing with psychological investigations on the measure of individual abilities will constitute the most important section of the journal.

In these two numbers, besides the reviews, there are articles on special training courses for teachers recently established in Italy and on the forms to be used in the medical examination of school children made with the object of determining their fitness for special trades. Included is also a report regarding the International Congress of Technical Teachers which was held in Rome, May, 1936.



THE ANATOMY OF PERSONALITY.

By Clements C. Fry and Howard W. Haggard. Harper and Bros., New York. \$2.00. 8 x 5; xi + 357 + 1 plate; 1936.

This is an attempt to analyze, describe and classify human personality. According to the authors, the elements of personality are: the physique, the impulse or driving force, the intelligence, the temperament, the ego. Each of these elements is discussed at length in separate chapters. These also include numerous examples to illustrate the variations and combinations of elements which characterize the different types of "normal" and psychopathic personalities. The outstanding fault of the book is that nowhere do the authors state exactly what they mean by the terms personality, temperament, etc. Aside from this, the book is to be regarded as a well written, interesting, and occasionally amusing popular version of numerous facts and theories regarding the psychological aspect of human constitution.



AFRICA'S GOD. I—*Gold Coast and Its Hinterland. Anthropological Series of the Boston College Graduate School, Vol. I, No. 1.*

By Joseph J. Williams, S.J. Boston College Press, Chestnut Hill, Mass. \$1.00. 9½ x 6½; 86; 1936 (paper).

The form of early religion and the lines of its development among the natives of the Gold Coast and its hinterland is the subject of this exposition which takes the form of a debate developed by means of quotations from persons who have lived and worked among these tribes and who are therefore considered to be "competent authorities" on the subject.

The conclusion reached is that there is, in general, on the Gold Coast Olympus a Supreme Being with a group of subservient spiritual entities, and another lower group of spiritual entities—the ancestral spirits.

There is a bibliography and author and subject indexes.



HUMAN GEOGRAPHY. *The Pacific Lands.*

By J. Fairgrieve and Ernest Young. George Philip and Son, London. 2s. 6d. net. 7½ x 4½; iv + 226; 1936.

Written primarily for use in intermediate

and secondary schools, this text covers briefly for the lands in and surrounding the Pacific Ocean such topics as winds, temperatures, climate, mountains, rivers, vegetation, minerals, foods, people, religions, and occupations. The authors have endeavored to present these facts "in such a way that they are seen to make a little clearer some of the problems of the modern world," and it may be said that their aim has been reasonably achieved.



### ZOOLOGY

THE SPONGES OF THE BAY OF NAPLES, PORIFERA INCALCABIA. *With Analyses of Genera and Studies in the Variations of Species.*

By G. C. J. Vosmaer. Edited by C. S. Vosmaer-Röhl and M. Burton. *Martinus Nijhoff, The Hague.* Gld. 125 (paper); Gld. 135 (cloth). 134 x 10; 875 + 69 plates; 1932-1935.

This magnificent monograph is a contribution of major importance to the permanent literature of zoology. It is greatly to the credit of the Dutch that they have financed, at what must have been great expense, the really adequate publication of Vosmaer's remarkable work.

The monograph is fundamentally taxonomic in character. Some 30 odd genera are systematically dealt with. Special attention is devoted to the boring sponges belonging to the family Clionidae. But the work is of deeper import biologically than straightforward taxonomy. Professor Vosmaer was much interested in the problems of organic variation, and includes a great mass of pertinent and significant data on variation in the forms with which he is dealing. Some day this mass of material will be tapped to good purpose by the theoretical biologists studying evolution.

In many ways the outstanding feature of these three volumes is the series of superb plates, mostly in color, and beautifully reproduced from paintings of the living sponges.

Altogether we have here a worthy monument to the memory of a great zoologist. It will stand for a long time as a solid reference work.

ARABIAN ADVENTURE to the Great Nafud in Quest of the Oryx.

By Douglas Carruthers. H. F. and G. Witherby, London. 8s. 6d. net. 84 x 54; xii + 208 + 33 plates and 2 maps; 1935.

An extraordinarily interesting book, written in 1934 about a trip into central Arabia in 1909, in successful search for one of the shyest of mammals, the White Oryx of Arabia, first named *Antelope oryx* by Pallas in 1777, and nearly a century later accurately described by John Edward Gray as *Oryx beatrix*. It seems as certain as any such matter can ever be that this creature furnished the factual basis for the fabled unicorn, for while it has two horns, in certain lights and aspects it appears to have but one. The author, a friend of T. E. Lawrence, presents an unusual combination of erudition, love of travel and adventure, and first-rate literary ability.

The Oryx is a strange beast, thoroughly adapted to desert life in the most arid regions and able to survive definitely only because of these adaptations.

Of water the Oryx are independent, but moisture they must have, and of necessity they follow the pasture that holds it. The most succulent grasses, such as *Nursi* and *Sabat* are doubtless their principal food, but the young shoots of tamarisk and other shrubs are sought for in spring. Even more desired are those peculiar juicy parasites that grow on the roots of the desert shrubs, especially the tamarisk and *ghadba*. There are two sorts, the red *Tarshush*, *Cynomonium cocconeum*, and the yellow *Philipsia lutea*. These long spadices may be as much as 18 to 24 inches long, and are full of liquid, especially the major portion below the sand. The Oryx dig for these so as to get at the best and most succulent end. Besides these, there are numerous other bulbous and tuberous plants which supply the moisture which these drinkless Antelope must have. Regarding the term "drinkless," some explanation is needed. It is quite obvious that the Oryx, as indeed all animals inhabiting this arid region, must be able to endure indefinitely without a proper drink. In no case is there any possibility of there being surface water, such as rain-pools caught in hollow rocks, for more than a few months in the year. In many districts even this chance of a brief drinking-hour is withheld. The Oryx, therefore, can be said to be entirely independent of water, although they will drink if given the opportunity to do so.

The photographs illustrating the volume are remarkable. There is an excellent bibliography and also an index.

THE FLOUR BEETLES OF THE GENUS *TRIBOLIUM*. United States Department of Agriculture Technical Bulletin No. 498.

By Newell E. Good. U. S. Government Printing Office, Washington. 10 cents. 9½ x 6; 57; 1936 (paper).

In recent years a rising interest in the flour beetles of the genus *Tribolium* has been apparent. This interest has developed largely within two groups of investigators: the economic entomologists, who have had to cope with the control of these beetles as serious pests in flour mills, and the experimental population students, who have found in *Tribolium* a useful animal for the study of their problems. The present paper by Good is designed to lay certain general foundations about *Tribolium* which will be useful to both of these groups as a background for their work. The author discusses in detail for the first time the taxonomy of the genus and shows, among other things, that the red-rust flour beetle commonly known as *Tribolium ferrugineum* Fabr., is more properly designated *Tribolium castaneum* Herbst. This section is followed by a consideration of the history and economic status of *Tribolium*; a detailed account of the life-cycle of our two American species *Tribolium confusum* and *T. castaneum*; the interrelations of the flour beetles with other animals, and control measures useful in checking *Tribolium* infestations of stored products. A considerable amount of new data appears at various places throughout the text. This is especially true of the section on life-cycles where Doctor Good presents some original records on oviposition and mortality.

To certain people this paper will be welcomed as an important reference work. It summarizes competently a great deal of information about the flour beetles, and, unlike many economic studies, maintains a sound, biological approach throughout. An outstanding feature is the excellent bibliography which lists some 108 titles all directly or indirectly related to *Tribolium*. The illustrations are likewise of high standard.



PAPERS FROM TORTUGAS LABORATORY OF

Vol. XXIX. Carnegie Institution of Washington Publication No. 452.

Carnegie Institution of Washington. \$4.75 (paper); \$5.75 (cloth). 10 x 7; 386 + 27 plates; 1936.

Valuable contributions in the field of marine biology are presented in this collection of fourteen papers covering studies on the biology of Tortugas corals; parasitic copepods from the Dry Tortugas; the ciliates of sea-urchins; intersexuality in the crustacea and the mechanism of chela differentiation in the crustacea; regeneration, cytology, metamorphosis of particular marine forms; electrical resistance of *Valonia*; the water exchanges of living cells; the effect of light on orientation and stability of young plectognath fish.

The longest and most detailed report is made by E. M. Thorp on the calcareous shallow-water marine deposits of Florida and the Bahamas. Mechanical analyses to determine the percentages of marine deposits and microscopical analyses to determine the organic constituents were made of 74 bottom samples and the results are listed in tabular form. The largest contribution of organically secreted calcium carbonate was made by the coralline algae. The principal non-calcareous mineral was quartz.

A paper by Oscar W. Richards examines critically the use of the heterogonic constant  $k$  in the formula  $y = b \cdot x^k$  when this is employed to represent the growth of a part ( $y$ ) of an organism with respect to the growth of the rest of the organism ( $x$ ). Data on the relationship between the size of the larger chela and the body of the male hermit crab *Caenobita clypeatus* are presented to show that a linear regression curve may give a more satisfactory fit than the above formula.



A MONOGRAPHIC REVISION OF THE GENUS *CEUTHOPHILUS*. (*Orthoptera, Gryllacrididae, Rhabdophorinae*) Biological Science Series, Vol. II, No. 1.

By Theodore H. Hubbell. University of Florida, Gainesville. \$3.75. 10½ x 7; 551 + 38 plates; 1936 (paper).

Cave-crickets and camel-crickets are the

genus *Centhophilus* (sub-family Rhaphidophorinae)—second largest genus of North American Orthoptera.

Rhaphidophorids are generally supposed by entomologists to be uncommon, and are rarely seen by other persons. This is largely the result of their secretive habits; active by night, they spend the day in close concealment. They have no song to attract attention, and are rendered inconspicuous by their sober coloration and immobility in the presence of strong light. Most of the species inhabit woodland, seeking shelter among the dead leaves and other debris of the forest floor; others are grassland- or even desert-dwellers, and these commonly dig holes in the ground, or take refuge in the burrows of larger animals or in natural cavities, from which they may emerge on nocturnal forays. Many species find the twilight zone in the entrances of caves a congenial habitat, and in such places these insects often congregate in large numbers.

It is probable that a large number of species are still to be discovered, but the present volume is the only comprehensive treatise on the taxonomic data of the group as known to date, the last account having been published in 1894. Many important changes have been made in classification since that time, and many new species described. The author has indeed produced here a superb piece of sound taxonomic work. There is a good bibliography and an index.

#### GENERAL ENTOMOLOGY.

By Robert A. Wardle. P. Blakiston's Son and Co., Philadelphia. \$2.25. 8½ x 5½; vii + 301; 1936.  
This small entomological text,

... is intended for students to whom the subject of entomology represents merely one or two courses of the many that comprise their training for the profession of zoology or agriculture, and who do not require the detailed knowledge of insect morphology and insect classification that is essential to the professional entomologist, but do require a broad appreciation of the basic principles of the subject.

In general, the book lives up to this standard set in the preface and should find friends among the group for which it is written. Despite its small size the author has succeeded in treating, in moderate detail, most of the important aspects of entomology, viz., anatomy, development (both embryonic and post-embryonic), physiology, behavior, taxonomy and characteristic group features, etc. On the

whole the volume leaves the reader with a fairly rounded survey of the subject. A novel, and in some ways courageous, feature of the book is the listing of contemporary entomologists, who are, in the opinion of the author, the recognized authorities in their respective fields. Certain references are cited in the text but no comprehensive bibliography or glossary is included. The illustrations are few and not particularly distinctive.

#### AN ANALYSIS OF THE *De Generatione Animalium* OF WILLIAM HARVEY.

By Arthur W. Meyer. Stanford University Press, Stanford University, Calif. \$3.00. 8 x 4½; xx + 167 + 11 plates; 1936.

Once an individual acquires prominence in a particular field of activity, it is usually assumed that his judgment is infallible on any other subject. At present, for example, the opinions of eminent astrophysicists on religion, politics and general science are regarded as sacrosanct.

To a much lesser degree the same sort of thing has happened in the case of Harvey. The great discovery presented in the *De Motu Cordis* has been considered a sufficient guarantee that *De Generatione Animalium* is of the same calibre. Huxley regarded it as a 'remarkable work which would give him claim to rank among the founders of biological science had he not been the discoverer of the circulation of the blood.' In this analysis, Meyer shows that such hyperbolic praise is really not justified. With all due respect to Harvey, the author finds very little to distinguish this treatise from those of Harvey's predecessors or contemporaries. Even the famous phrase attributed to him *Omne vivum ex ovo* is a misquotation. To Harvey's credit it must be said that he avoided a number of the superstitions then in vogue. Still he was unable to perceive the facts of reproduction any clearer than the other investigators of the time.

Harvey's greatness does not suffer from this critical analysis of *De Generatione Animalium*. The author at all times maintains a respectful attitude and his criticism is mild and impersonal. For this, he deserves great credit. The book should be required

reading for all science students. Due to the teaching methods still in vogue, most of the students cannot liberate themselves entirely from the awe for a great name.



THE AMERICAN WOODCOCK *PHILOHELA MINOR* (GMELIN). *Memoirs of the Boston Society of Natural History, Volume 9, No. 2.*

By Olin S. Pettingill, Jr. *Boston Society of Natural History, Boston.* \$4.75 bound; \$3.50 paper. 12 x 9½; 225 + 10 plates; 1936.

The American woodcock is a bird well-known in eastern North America as a table delicacy, but perhaps fewer people are well acquainted with its interesting life history. The perusal of this monograph however gives the reader a ring-side seat whereby he can watch as though at first hand the development of individuality in this bird. The courtship performance of the woodcock is unique and is described in detail, and other characteristics are just as adequately treated. This compact assemblage of material is a result of intensive and intimate field studies of the bird, a good review of the literature on the subject, the returns from a thousand questionnaires sent out requesting information relative to abundance, migration and breeding, and the examination of skins and skeletons and dissection of specimens. The monograph is beautifully illustrated.



PIGEONS AND SPIDERS (*The Water Spider*).

By Maurice Maeterlinck. Translated by Bernard Miall. *W. W. Norton and Co., New York.* \$1.75. 7½ x 5½; 128; 1936.

This entertaining volume is largely about the Argyronet, a spider that chooses to envelope itself in a "silver" diving bell and carry on its activities mostly beneath the water. Maeterlinck first became acquainted with these spiders when as a boy he observed them in a moat surrounding his grandfather's garden. With his grandfather, who must have been something of a naturalist, he studied them in a "natural

history cabinet"—a glass jam pot. Sixty-two years later the writer renewed his interest in these creatures when there happened to reach him from Belgium a jam pot "which bore a magical resemblance to the jam pot of my childhood, and in this too half a dozen bubbles of mercury were in motion, just like those of my premonitory vision." Of equal interest is the essay on pigeons. Maeterlinck cannot resist debunking them somewhat but tells many amusing things about them and discusses their family life, their habits, and sense of orientation. As one would expect both of these essays include philosophical discussions on instinct, intelligence, nature, and life. Many questions are asked, but very few does the author really attempt to answer.



THE INTERPRETATION OF THE ZONES ON SCALES OF SALMON, SEA TROUT AND BROWN TROUT. *Rapports et Procès-Verbaux des Réunions Volume XCVII.*

By T. H. Järvi and W. J. M. Menzies. Andr. Fred. Høst and Fils, Copenhagen. Kr. 4.00. 10½ x 8½; 63; 1936 (paper).

The technique of scale reading for age determination of three salmonoid fishes is clearly described in the text of this report and is closely supplemented with photographic illustrations. During the first summer the scale ridges are well spaced and well formed, but thereafter summer is denoted by a wide growth zone and winter by a slow growth zone of finer and more closely spaced ridges. Spawning periods may also be read from the scales. During the ascent of the rivers to the spawning grounds reserves of nourishment stored in the scales are absorbed, thus destroying scale material to a greater or less extent. Normal growth is resumed again on return to the sea. Some of the pitfalls or complications of scale reading are also described. The authors are both recognized authorities in this field of research.



COLLEGE ZOOLOGY. *Fourth Edition.*

By Robert W. Hagner. *The Macmillan*

Co., New York. \$3.50.  $8\frac{1}{2} \times 5\frac{1}{2}$ ; xvi + 742. 1936.

The fourth edition of this well-known and extensively used zoölogical textbook has been revised by rewriting many of the chapters; by expanding the discussions of the Protozoa, Arthropoda and the frog; by adding new chapters on the "Relations of Protozoa to Man" and on "Parasitism in Animals"; by enlarging the glossary and adding cross-page references to it, and by including a number of new illustrations. It is interesting to note that the author still holds to the "type" method of presentation—the development of the subject from the viewpoint of taxonomic groups. This procedure, once conservative, is now becoming more radical due to the increasing number of books based on "principles"—the organization of the subject about certain concepts and theories. As to which method of presentation is superior it is difficult to say. It can be predicted, however, that this text will continue to enjoy popularity in its fourth edition.



BIRDS OF CAPE YORK PENINSULA. *Ecological Notes, Field Observations, and Catalogue of Specimens Collected on Three Expeditions to North Queensland.*

By Donald F. Thomson. Angus and Robertson, Sydney. 1s. 6d.  $9\frac{1}{2} \times 6$ ; 82 + 15 plates; 1935 (paper).

During the course of expeditions carried out over a period of three years into North Queensland for anthropological work, a study of the birds of the region was made as a side issue, largely from the standpoint of geographical distribution. There is a brief descriptive account of the physical characteristics of the Cape York Peninsula and a classification of the country into five principal flora-fauna association areas. 183 species of birds were observed here. It is interesting to note that less than half of this number are endemic Australian species while the remainder have a range extending to New Guinea or beyond. An index of the common as well as scientific names is included.

SEASHORE ANIMALS OF THE PACIFIC COAST.

By Myrtle E. Johnson and Harry J. Snook. The Macmillan Co., New York. \$6.00.

$9\frac{1}{2} \times 6\frac{1}{2}$ ; xiv + 659 + 11 plates; 1935.

A reprint of a volume which first appeared in 1927. It is a non-technical, illustrated account of the structure and habits of the common seashore animals of the west coast of the United States. Being replete with interesting information and excellently illustrated with numerous line drawings, half-tones and colored plates, teachers of elementary biology in colleges and high schools will find the volume highly useful. Naturalists, particularly those visiting the west coast, will find it a desirable library book. Unfortunately its size and weight do not make it handy for field work. The authors have included sections on collecting and preserving marine forms, a lengthy reference list, a glossary and an index.



LEÇONS DE ZOOLOGIE. *Protozoaires flagellés. Actualités Scientifiques et Industrielles*, 296.

By M. Prenant. Hermann et Cie, Paris. 12 francs.  $10 \times 6\frac{1}{2}$ ; 56; 1935 (paper).

LEÇONS DE ZOOLOGIE. *Protozoaires infusoires ciliés. Actualités Scientifiques et Industrielles*, 295.

By M. Prenant. Hermann et Cie, Paris. 15 francs.  $10 \times 6\frac{1}{2}$ ; 77; 1935 (paper).

These two books, members of the rather lengthy series surveying the invertebrates, present certain orthodox taxonomic, morphological and physiological data on the flagellate and ciliate Protozoa. As with previous volumes the standard, while adequate, is not especially distinctive and one feels that just another textbook discussion of two animal groups has been created. Both books contain a number of mediocre, time-worn illustrations of familiar forms and both have bibliographies of a few selected titles. It seems certain that if these paper-bound brochures get the type of service usually accorded textbooks they will last about one semester if not less.

ZOOLOGICA. *Scientific Contributions of the New York Zoological Society. Volume XXI, Part I, Numbers 1 and 2. Containing following articles: The Reproductive Habits of the North American Sunfishes (Family Centrarchidae), by C. M. Breder, Jr.; Polychaetous Annelids from the Vicinity of Non-such Island, Bermuda, by A. L. Treadwell.*

New York Zoological Society, New York.

\$1.00. 10½ x 7; 68 + 10 plates; 1936 (paper).

Breder's monograph on the sexual and breeding behavior of the common sunfishes is a valuable and important contribution. In addition to his own original observations, which bring out many novel points, he thoroughly and critically reviews the older literature. It is an interesting finding that the primitive forms make the most elaborate nests and give more parental care than the higher forms, where the nests are much simpler.

Treadwell lists and describes 17 old and 8 new species of polychaetes from Bermuda.



OUTLINES OF GENERAL ZOOLOGY. *Third Edition.*

By *Horatio H. Newman*. Macmillan Co., New York. \$3.50. 8½ x 5½; xxvii + 661; 1936.

A LABORATORY MANUAL FOR GENERAL ZOOLOGY.

By *Katherine McC. Roehl* in collaboration with *H. H. Newman*. Macmillan Co., New York. \$1.00. 8½ x 5½; vii + 99; 1936.

In this new edition of Newman's standard and successful text "much of the book has been completely rewritten, but a great deal of it remains unchanged" or only slightly modified. Summaries at the end of chapters are a new feature.

The laboratory manual was especially designed for use with the *Outlines* but the authors believe that it should fit any textbook of general zoology or animal biology.



A LABORATORY MANUAL OF INVERTEBRATE ZOOLOGY. *Fifth Edition, Revised.*

By *Gilman A. Drew*. Revised by *James A. Dawson and Leonard P. Sayles*. W. B.

Saunders Co., Philadelphia. \$2.25 net. 7½ x 5; 276; 1936.

Rapidly becoming a classic of the invertebrate dissection laboratory, this book (earlier reviewed in Q.R.B., 1929: 4; p. 280) has been revised,

... for the purpose of modifying and enlarging the fourth edition. Some important changes in classification have been made and the instructions for the study of certain commonly used animals have been made more complete. Such errors as had not been eliminated in earlier editions have, it is hoped, been corrected. The glossary has been thoroughly rewritten and revised.



DIE BLATT-MINEN MITTEL- UND NORD-EUROPAS. *Bestimmungs-Tabellen aller von Insekten-Larven der verschiedenen Ordnungen erzeugten Minen. Lieferung 2.*

By *Martin Hering*. Gustav Feller, Neubrandenburg. 9½ x 6½; 113-224 + 1 plate; 1936 (paper).

A continuation of an identification list, with some illustrations, of leaf burrows. Arranged alphabetically by plant host this number includes from *Bryonia* (Curcubitaceae) to *Filipendula* (Rosaceae). The first number of the work was noticed in this REVIEW, Vol. 11, p. 239.



HEDGE FOLK IN TWILIGHT.

By *Phyllis Kelway*. Longmans, Green and Co., New York. \$2.50. 7½ x 5½; xi + 178 + 22 plates; 1936.

At one time or another Miss Kelway has made friends with a number of wild creatures such as dormice, hedgehogs, a heron, and a most amusing brown owl. She now tells us of her experiences in a pleasant, unpretentious way. Her book won't add much to the general body of scientific knowledge, but it is good reading.



A SHELLAC PATENT INDEX.

By *R. W. Aldis*. Indian Lac Research Institute, Namkum, Ranchi, Bihar and Orissa, India. Rs. 2/8. 9½ x 7½; iv + 115; 1935.



This book gives lists of parents concerning the manufacture and use of shellac. It is clearly arranged and there is a good index.



DINOFLAGELLATA OF THE SAN FRANCISCO REGION. *On the Skeletal Morphology of Two New Species, Gonyaulax Catenella and G. Acatenella.* University of California Publications in Zoology. Vol. 41, No. 4.

By W. Forest Whedon and Charles Atwood Kofoid. University of California Press, Berkeley. 10 $\frac{1}{2}$  x 6 $\frac{3}{4}$ ; 25-34; 1936 (paper).

SPAWNING HABITS OF THE MUSSEL MYTILUS CALIFORNIANUS CONRAD. *With Notes on the Possible Relation to Mussel Poison.* I. University of California Publications in Zoology, Vol. 41, No. 5.

By W. Forest Whedon. University of California Press, Berkeley. 10 $\frac{1}{2}$  x 6 $\frac{3}{4}$ ; 35-44; 1936 (paper).

NEW SPECIES OF SPIONIDAE (ANNELIDA POLYCHAETA) from the Coast of California. University of California Publications in Zoology, Vol. 41, No. 6.

By Olga Hartman. University of California Press, Berkeley. 10 $\frac{1}{2}$  x 6 $\frac{3}{4}$ ; 45-52; 1936 (paper).

SOME NEW AND LITTLE KNOWN AMPHIPODS OF CALIFORNIA. University of California Publications in Zoology, Vol. 41, No. 7.

By A. L. Alderman. University of California Press, Berkeley. 10 $\frac{1}{2}$  x 6 $\frac{3}{4}$ ; 53-74; 1936 (paper).

CROTALUS MITCHELLII, THE SPECKLED RATTLESNAKE. *Transactions of the San Diego Society of Natural History. Volume 8, Number 19.*

By Laurence M. Klauber. Society of Natural History, San Diego, Calif. 10 $\frac{1}{2}$  x 6 $\frac{3}{4}$ ; 36; 1936.

NOTES ON BIRDS IN RELATION TO THE FAUNAL AREAS OF SOUTH-CENTRAL ARIZONA. *Transactions of the San Diego Society of Natural History, Volume 8, Number 18.*

By A. J. van Rossem. Society of Natural History, San Diego, Calif. 10 $\frac{1}{2}$  x 6 $\frac{3}{4}$ ; 28; 1936.



## BOTANY

THE MUSHROOM HANDBOOK.

By Louis C. C. Krieger. The Macmillan

Co., New York. \$3.50. 7 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; xiv + 538 + 32 plates; 1936.

An excellent hand book which seems to be complete in every department. The novice will find it easily within his comprehension. After becoming thoroughly familiar with the section on mushrooms *safe for the beginner* he can confidently venture tackling the more difficult varieties. The section on poisonous mushrooms is so clear that one can scarcely fail to recognize these forms. The volume, however, is far more than a key to the mushroom family. Considerable space is given to conditions under which mushrooms grow and thrive, the habitats which the different varieties prefer, and the life history and general characteristics of mushrooms—even to bio-luminosity and monstrosities. The section on growing mushrooms artificially gives useful information to those wishing to venture into this field. The latter part of the book (pp. 181 to 454) is devoted to a systematic account of selected larger fungi with detailed descriptions of 238 types and a classification chart. There is also included in the volume some excellent recipes for cooking mushrooms, an index to the literature for identification of the larger fungi, a list of the principal authors of fungus species, a lengthy bibliography, a glossary and an index. The excellent illustrations—126 black and white drawings and photographs, and 32 colored plates from the author's paintings—add immeasurably to the value of the book.



J. ARTHUR HARRIS: *Botanist and Biometrician.*

Edited by C. Otto Rosendahl, Ross A. Gortner and George O. Burr. University of Minnesota Press, Minneapolis. \$2.50. 9 $\frac{1}{2}$  x 6; viii + 209; 1936.

Dr. Harris (1880-1930) started his biological work with a paper on crayfish as an undergraduate at Kansas University, later taking his Ph.D. in botany at Washington University, St. Louis. He soon became interested in the mathematical approach to biological problems and after spending two winters in Karl Pearson's laboratory became a pioneer in introducing statistical methods into botanical problems.



Though the present volume is disappointing as a biography it contains the following previously unpublished papers of interest to workers in the fields represented: Some Chemical Factors of the Soil That Influences the Distribution of Desert Vegetation, by J. A. Harris and Vernon A. Young; The Distribution of Errors of Analyses, by J. A. Harris and Alan E. Treloar; The Length and Weight of the Newborn Infants of Various Nationalities, by J. A. Harris, Alan E. Treloar, and Borghild Gunstad; The Relationship Between Number of Pregnancies and Number of Births in Man, by J. A. Harris and Borghild Gunstad; The Measurement of the Individuality of Women with Respect to Their Capacity for Bringing the Foetus to Term, by J. A. Harris and Borghild Gunstad; Fecundity in the American-Born and Foreign-Born Inhabitants of New York City, by J. A. Harris and Borghild Gunstad; A Great Institute for the Study of the Psychology of the Mule, by J. A. Harris.

This last paper is a satire on the red tape in most government and university research departments.



**MEDICAL MYCOLOGY. *Fungous Diseases of Men and Other Mammals.***

By Carroll W. Dodge. C. V. Mosby Co., Saint Louis. \$10.00. 10 x 6½; 900; 1935.

Many and varied are the types of fungous diseases of man, among them being such commonly known infections as dandruff, acne, ringworm, herpes eczema, etc.

This authoritative treatise is primarily a taxonomic reference work for the medical man. Introductory chapters cover general morphology and physiology of the fungi; the technique involved in culture media and the isolation of microorganisms; microscopy, and botanical nomenclature. The taxonomic data of the succeeding chapters are followed in the case of each group of microorganisms under consideration by a complete bibliography. This is the first time a bibliography so thoroughly covering this field has ever been available.

**QUELQUES RÉSULTATS STATISTIQUES NOUVEAUX CONCERNANT LA FLORE VASCULAIRE DE QUÉBEC. *Contributions du Laboratoire de Botanique de l'Université de Montréal. No. 26.***

By Frère Marie-Victorin. Institut Botanique, Université de Montréal, Montréal. 15 cents. 9 x 6; 8; 1935 (paper).

This is a statistical study of the distribution of vascular plant species in the Province of Quebec. Of 142,600 known species 1917, or one and one-third per cent, have been found in this territory. This percentage has been estimated to be about the average for a unit of this area. The predominant families, *i.e.*, those with the most species represented, are the Cyperaceae, the Compositae, and the Gramineae.



**MORPHOLOGY OF VASCULAR PLANTS. *Lower Groups (Psilophytales to Filicales).***

By Arthur J. Eames. McGraw-Hill Book Co., New York. \$4.00. 9 x 6; xviii + 433, 1936.

In this text book, the outgrowth of the author's experience in teaching, there is made available to the student the important changes in interpretation and classification of the morphology of vascular plants which recent studies have brought about. It is divided into two parts, the first dealing with the lower and the second with the higher groups. The view point is that of broad comparative study with the development of a natural classification and phylogenetic relationship as the goal. Emphasis is placed upon the range of structure within the group. Individual forms are not treated in detail, and cytological aspects have been largely omitted, as have many details of anatomical structure. Classification is built up as the groups are studied, and the goal of the study, a classification that is as closely natural as possible, is attained only at the end of the book. The living and fossil forms for most major groups are treated separately. Each chapter has a section devoted to discussion and summary and concludes with a bibliography. The volume is generously illustrated with excellent figures and photographic reproductions and contains a short general

bibliography and a detailed index. A sound and useful book.



BLACK ROCK FOREST PAPERS, Vol. 1. No. 1, *A Method for Determining the Nutrient Needs of Shade Trees with Special Reference to Phosphorus*, by Harold L. Mitchell. No. 2, *The Relative Feeding Power of Oaks and Maples for Soil Phosphorus*, by H. L. Mitchell and R. F. Finn. No. 3, *A Chestnut Oak Volume Table for the Hudson Highland Region*, by H. H. Tryon and R. F. Finn. No. 4, *The Effect of Varied Solar Radiation Upon the Growth, Development and Nutrient Content of White Pine Seedlings Grown Under Nursery Conditions*, by H. L. Mitchell. No. 5, *Differential Browsing by Deer on Plots Variously Fertilized*, by H. L. Mitchell and N. W. Hosley.

Black Rock Forest, Cornwall-on-the-Hudson, New York. 11 x 8½; 27; 1935-36 (paper).



## MORPHOLOGY

NEUROEMBRYOLOGY. *An Experimental Study.* By Samuel R. Derwiler. Macmillan Co., New York. \$3.75. 8½ x 5½; x + 218; 1936.

This book, by one of the leading investigators in the field of neuroembryology, is designed "to discuss more specifically problems concerning the growth of peripheral nerves, factors influencing the proliferation of nerve cells, as well as the capacity of the developing nervous system to undergo structural and functional adaptations in response to new conditions experimentally imposed upon it." Experimental work of this nature has been largely upon *Amblystoma*, the frog and the chick. In the first 13 chapters of the book the author discusses the work of various investigators as well as his own important findings. From the final chapter on summary and interpretations, we give brief extracts:

.... experimental evidence is presented.... to show that in embryos from which the myotomes have been removed, so that the axial musculature is entirely wanting, motor nerve outgrowth is not sup-

pressed. Only the segmental arrangement is destroyed.

The results of these and other experiments show that the brachial correlation mechanism is definitely limited within the cord and cannot be extended under experimental conditions.

.... experiments dealing with correlated limb function.... demonstrate that any spinal or cranial somatic motor nerves are capable of bringing about movements in grafted limbs. These movements, however, are always stereotyped and associated with those characterizing the region into which the limb has been grafted.

Evidence is presented to show that alteration in the number of sensory fibers entering the central nervous system influences cell division and differentiation in the centers penetrated by these fibers. When a peripheral sensory area such as the eye or nasal epithelium is ablated, or is augmented by grafting a supernumerary organ adjacent to the normal, the number of primary sensory neurons is changed.

.... local regions or peaks of accelerated proliferation within the brain wall influence the ingrowth of sensory nerve roots.

On the basis of the experimental results, a discussion is given of the causes of variations in the number of segmental nerves contributing to the limb plexus in different groups of vertebrates.

Experiments are also described in which reflex behavior is modified by the excision of certain coordinating projection tracts (Mauthner's fiber) present in fishes and aquatic amphibia. The cell bodies which develop these fibers lie in the medulla and their axons course through the entire length of the spinal cord.

A lengthy bibliography and an author and subject index are included in the volume.



## A TEXTBOOK OF HISTOLOGY.

By Joseph Krafka, Jr. Williams and Wilkins Co., Baltimore. \$2.50. 9 x 6; vii + 246 + 1 plate; 1936.

This is a clearly-written and well-organized textbook of histology which attempts to picture, in not too great detail, the principal cellular features of human tissues and to relate these features with other fields of biology. The author is insistent that histology shall assume a position in modern biology comparable to that held by embryology, genetics, physiology, "evolution," biochemistry and comparative anatomy. He makes these points in an evangelistic fashion in the preface and obviously hopes that his book will do much towards placing histology on a more-appreciated plane. Whether this will be the case remains to be seen. In any event, the book will find users among the

group requiring an introduction to the facts of the subject even though they may not envisage the relation of microscopic anatomy to "diets," "public health," "popular medical education," "education," "criminology" and "social adjustment." The volume is indexed, but has no bibliography. The illustrations, which are mostly from pen and ink drawings, struck the reviewer as being of rather mediocre quality.



#### HOW ANIMALS DEVELOP.

By C. H. Waddington. W. W. Norton and Co., New York. \$2.00. 8 x 5½; 128 + 7 plates; 1936.

This is a brief account of the science of embryology written for the "intelligent layman and the elementary student." Such features as fertilization and cleavage, germ-layer formation, organization centers of the embryo and the relation of these centers to embryonic pattern and differentiation, and later developmental specializations are discussed in the text. Unlike most books of this nature the author emphasizes the dynamic and experimental aspects of ontogeny and so imparts to his subject an interest which otherwise might be lacking. For example, he discusses such problems as vital staining and its bearing on an understanding of gastrulation; the "organizer" experiments of the Spemann group; the rôle of genes in development, etc. An excellent example of sound popularization of science.



#### ATLAS OF HUMAN ANATOMY with Explanatory Text.

By Jesse F. Williams. Colored illustrations by Franz Frohs, Max Brödel and Leon Schlossberg. Barnes and Noble, New York. \$2.00. 8½ x 5½; 64; 1935.

The significant feature of this little atlas is the series of beautifully colored anatomical diagrams which cover twenty-five pages. As the book has an appeal to the inquiring layman as well as to the student of anatomy, the diagrams are labelled

with the common names, followed by the Latin names in parenthesis. In the twenty-five initial pages of explanatory text, an effort is made to outline the workings of the anatomical systems, with frequent references to the accompanying diagrams.

The book is admirably suited to its purpose. However, it is not, and does not attempt to be, a textbook on anatomy. It is an accurate, beautiful, and comparatively complete little picture book of human anatomy.



#### ANIMAL MICROLOGY. *Practical Exercises in Zoological Micro-Technique.*

By Michael F. Guyer. With a chapter on drawing by Elizabeth A. (Smith) Bean. The University of Chicago Press, Chicago. \$2.50. 8½ x 6; xvi + 331; 1936.

The fourth edition of this popular text on histological technique (earlier noticed in Q.R.B., 1931: 6; p. 111) has been revised primarily by the introduction of a chapter (vii) on the dioxan method. By using dioxan, a liquid miscible both with melted paraffin and water, certain steps in the preparation of tissues, e.g., absolute alcohol and xylol washings, may be omitted. This, according to the author, makes for a quicker and more simplified procedure and so justifies itself. Other minor changes and additions, too numerous to list, have been made throughout the text. The book's well-deserved success in the past will continue.



#### SIX CONFÉRENCES D'HISTOPHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Substance Osseuse. Ossification Endochondrale. Alvéole Pulmonaire. Paroi Artérielle. Micro-incinération. Histspectrographie.*

By A. Policard. Masson et Cie, Paris. 15 francs. 9½ x 6½; 105; 1935 (paper).

This book incorporates six lectures presented before the Medical Faculties of Buenos Aires in May, 1935. The subjects were: the formation of bone; the elementary processes of endochondral ossification; the alveolar membrane of the

lung and its histophysiological mechanisms; the arterial wall and some of its histophysiological mechanisms; the method of microincineration of cells and tissues; a new technique in histochemistry: histospectrography. The technique described in the last lecture was devised by the author and A. Morel in 1931 and 1932.



THE STUDY OF ANATOMY. *Written for the Medical Students. Third Edition, Revised and Enlarged.*

By S. E. Whitnall. William Wood and Co., Baltimore. \$1.75. 7½ x 4½; viii + 113; 1936.

This useful little volume in its third edition (previously mentioned in Q. R. B., Vol. 9, No. 3) has been revised and enlarged. Its *raison d'être* is "to impress the medical student with the fact that human anatomy must be considered in relation to (a) the living body, (b) physiology and other cognate subjects, (c) future clinical work, and that dissection of the cadaver is only one way of studying it." A capital book.



LES MOUVEMENTS MORPHOGÉNÉTIQUES DANS LE DÉVELOPPEMENT DES VERTÉBRÉS. *Actualités Scientifiques et Industrielles*, 303. *Exposés de Biologie (Embryologie et Histogénèse)*, V.

By Pierre Hatt. Hermann et Cie, Paris. 12 francs. 10 x 6½; 57; 1935 (paper).

This number of the *Actualités* presents a brief résumé of present knowledge concerning the morphogenetic processes in the early embryological stages of batrachians and birds. Three pages of detailed comparison between the first steps in the morphogenesis of birds and that of batrachians are included. There is a bibliography.



## PHYSIOLOGY AND PATHOLOGY

THE PATIENT AND THE WEATHER. *Volume 1, Part 2, Autonomic Integration.*

By William F. Petersen and Margaret E. Milliken. Edwards Bros., Ann Arbor, Mich. \$9.00. 10¾ x 8½; xxx + 781 + 2 folding charts; 1936.

In this second part of Vol. 1 (other volumes have been reviewed previously in this journal), the author presents evidence to show the association between changes in the atmosphere and modifications of individual physiologic reactions. In a first chapter he discusses asthenics and pyknics and the different morbidity found associated with the two physical types. The following chapters discuss meteorology and meteoropathology. Then the author presents the detailed study of four "normal" subjects: The influence of meteorologic changes on their metabolic activity, blood picture, blood pressure, temperature, weight, N. P. N. and other physical and psychic conditions. There are other chapters in which the author indicates the effect of weather changes on pregnant women, children, and individuals suffering from specific infections. All these and other facts led the author to conclude "that the organism adjusts to the meteorological environment by the three major components of the autonomic apparatus—chemical, endocrine, nervous." And, "the organism swings in a definite rhythm of increasing and decreasing oxidation, of increasing and decreasing pH, of increasing and decreasing metabolism, of increasing blood pressure, all clearly inter-related to the meteorologic environment." Finally, "while the organism seeks to maintain a proper balance by such a rhythm in the normal biological processes, the peaks and troughs are of clinical significance because here lack of prompt integration frequently leads to dysfunction, to disease, and finally to death."

The cases presented are excellent illustrations of this beautiful theory; however, as was remarked in our other reviews, the author fails to give the statistical evidence to support the theory. It is doubtful whether such evidence will ever be forthcoming from the author since in the preface he classifies it as a "scientific superstition" to believe "that a series of observations made at random, when compiled and leveled, have more signifi-

cance than the carefully controlled individual observation."

This is the most important volume of the series and deserves a careful study. The extensive bibliography will be found useful.



**BODY WATER.** *The Exchange of Fluids in Man.*

By John P. Peters. Charles C Thomas, Springfield, Ill. \$4.00 postpaid. 9 x 6; ix + 405; 1935.

An important treatise. In the preface the author says: "For many years the author with his associates has been engaged in studies of the distribution and movements of solutes and water in the human body. The experiments have involved such diverse fields of pathology and physiology that they may seem planless. The work has inevitably followed an opportunist course, turning to any clinical condition which promised however remotely to provide favorable experimental material and often enough abandoning the clinic entirely for the normal subject or the test tube." Nevertheless there have been certain definite guiding motives. Chief of these has been "the desire to test certain plausible hypotheses concerning the nature of restraints imposed by vital membranes in the body upon movements of fluid and electrolytes, and the influence which they have in the production of various clinical and pathological disturbances."

The work has been entirely restricted to the human subject and the present treatise represents a summary or survey of the whole field of the investigations in order to estimate the value of the original working hypothesis, to find gaps in the investigations, to perceive new points of experimental approach, and to attempt to construct a background for a more rational analysis of the functional pathology of renal disease. In order that the reader may obtain a general idea of the scope of the work we give the chapter headings: Chemical forces which control exchanges of fluid and solutes; the nature and movements of interstitial fluid and lymph; exchanges between blood and interstitial

fluids; serous fluids and transudates; exchanges between blood cells and serum; exchanges between tissue cells and interstitial fluids; water of oxidation and the losses of water and solutes through skin and respiratory passages; alimentary exchanges; the general nature of renal activity; renal excretion of filtrable organic solutes; renal excretion of water and inorganic salts; nervous and hormonal control of urine excretion.

In the bibliography and author index there are 875 titles.



**THE ADRENALS.**

By Arthur Grollman. *The Williams and Wilkins Co., Baltimore.* \$5.00. 9 x 6; xii + 410; 1936.

According to the preface, an attempt has been made in the present volume, "... to analyze the great accumulation of literature on the subject of the adrenals and present a working hypothesis from which the reader may start on his own efforts." The text material is divided into the following major divisions: Part I, "Anatomical Considerations"; Part II, "The Medulla"; Part III, "The Cortex," and Part IV, "Clinical Considerations." In the first part the gross and microscopic anatomy of the adrenals, as well as the morphology of the androgenic tissue (a portion of the adrenal which in certain pathological conditions gives rise to reproductive disorders) is discussed. Part II deals principally with the chemistry and pharmacology of epinephrine and the physiology of the medulla. Part III discusses such topics as the relation of the adrenal cortex to the general endocrine system; specific functions of the cortical hormone; the adrenals and metabolism, etc. The final part considers Addison's disease, adrenal tumors, the "adrenogenital syndrome" and other diseases of this gland.

This book is a competent review of many of the pertinent data about the adrenal glands and houses within its covers a wealth of carefully concentrated information presented in a logical fashion. It is certain that the volume will find a

warm welcome among endocrinologists. An excellent bibliography, adequate index and interesting historical summary of the field supplement the text.



**NEW FACES—NEW FUTURES.** *Rebuilding Character with Plastic Surgery.*

By Maxwell Maltz. Richard R. Smith, New York. \$3.00. 8½ x 5½; xv + 315; 1936.

The history of plastic surgery is a vivid one: it is strewn alike with charlatans and remarkably skillful surgeons. Unfortunately, the former are still with us. Fortunately, the latter are multiplying and along with their multiplication has come new technical skills. It is with the latter group and their achievements that this book concerns itself and, because of the human interest of the subject, it can be recommended as interesting reading. Using "before and after" pictures to supplement the text the author discusses some of the operations common to modern plastic surgery (e.g., hare-lip reconstruction, nose straightening, blemish removal, etc.) and shows how many of them have a favorable prognosis in respect of pulchritude as well as health and psychical well-being. The latter point is an interesting one. Apparently, the plastic surgeon frequently corrects unhappy mental disturbances traceable to prominent disfigurements when he improves the physical appearance of the patient. Many of the chapters are headed with such titles as, "Mr. Gump and Dick Tracy," "The knight of the silver nose," "A new deal for Cyrano," "Wrinkles, those damned democrats, won't flatter," etc. Did anyone beyond a mental age of six ever think this sort of thing was funny?



**EVANS' RECENT ADVANCES IN PHYSIOLOGY.** *Fifth Edition.*

Revised by W. H. Newton. P. Blakiston's Son and Co., Philadelphia. \$5.00. 7½ x 5½; xii + 500; 1936.

Some notion as to the revisions made in the present edition (fifth) of this book can

be obtained from the following statement by the present reviser:

Time may add charm to a work of art, and dignity even to a scientific textbook, but it deals harshly, almost vindictively with a work pretending to the title of "Recent Advances." This is nowhere more apparent than in the present volume, from which the unremitting pressure of new research has displaced several masterpieces of exposition. Only Chapters I, III, and VIII (coronary circulation; carotid sinus as a regulator of circulation; nerve conduction) have been carried over from the last edition, and even these have been greatly altered to bring them up to date, and they contain many new sections. The remaining eight chapters (cardiac muscle metabolism; carbonic anhydrase; foetal oxygen supply; sex hormones; chemical transmission at nerve endings; spinal reflex; urine secretion; nervous control of micturition) are quite new. . . .

It would be superfluous to say this is a good book. The fact that the volume has been through five editions since 1925 and that it has been enthusiastically reviewed on two occasions in this journal (Q. R. B., 1926: 1: p. 458 and 1927: 2: p. 461) amply attest the point.



**SÉROTHÉRAPIE ANTIPOLIOMYÉLITIQUE D'ORIGINE ANIMALE (S.A.P.)** *Seize Années d'Expérimentation Clinique.*

By Auguste Pettit. Masson et Cie, Paris. 30 francs. 10 x 6½; 271; 1936 (paper).

Pettit's horse serum has been used clinically in the treatment of poliomyelitis more extensively than any other horse serum. His experiments with this serum, begun in 1917, have continued to the present time. In 1929 he succeeded in preparing an immune serum from *Cynocephalus* and in 1932 successfully immunized a chimpanzee. The first part (56 pages) of this book describes the methods employed in the production of the immune sera from these animals.

The second part of the book is devoted largely to case histories from the files of physicians (with few exceptions French) who have used the Pettit serum in their practice. On the basis of these Pettit claims that among its attributes are (1) that with the injection of the serum in the preparalytic stage, subsequent paralysis and paresis do not occur; (2) that it blocks the infection and combats the ascent of

the virus; (3) that it diminishes the gravity of the sequelae when it does not suppress them entirely; and (4) it reduces the mortality from this disease by about one half. Some untreated cases are tabulated in comparison with treated cases but the numbers seem to us too small to test the efficaciousness of the serum. As the value of immune serum in the treatment of infantile paralysis is still a matter of debate it is to be regretted that more control cases were not included. However, as the stages of the disease at treatment and the route of administration of the serum are noted, it is well to have these cases on record.

A feature of the 28-page bibliography is the inclusion of abstracts of many of the items, and notes replying to criticisms or erroneous statements concerning the author's work.



OCCUPATION AND HEALTH. *Encyclopaedia of Hygiene, Pathology and Social Welfare*. Vol. I, A-H; Vol. II, I-Z.

International Labor Office, Geneva. U. S. Agents: World Peace Foundation, 40 Mt. Vernon St., Boston. £4; \$22 (paper). \$24 (cloth). 10 $\frac{1}{2}$  x 7 $\frac{1}{2}$ ; Volume 1, xxvi + 999; Volume 2, vii + 1310; 1930 and 1934.

The Health Section of the International Labour Office in Geneva has compiled this encyclopedia of Industrial Hygiene for the purpose of bringing together all the information available on the relation between working conditions and the health of the workers. The topics are listed in alphabetical order and the articles regard occupations, manufactured products, body organs, chemicals, diseases, etc. Some of the articles have been written by members of the staff of the Health Office, others are the contributions of medical specialists. All articles, in general, follow a definite pattern and contain descriptions of the industrial processes, the causes of disease, symptoms and diagnosis of the disease, statistical data on morbidity and mortality, comparative legislature enacted for the worker's benefit, and bibliography. As is to be expected, some articles are better

written and more complete than others. This is due to a number of factors, but principally because there is more information available for some topics than for others. The bibliography is generally limited to textbooks and general reference books. One criticism that must be made is that in some cases the findings of an author are quoted without giving any information on the whereabouts of the original report. The physician and human biologist will find these volumes useful.



#### ELEMENTARY HUMAN PHYSIOLOGY.

By Sherburne F. Cook. Harper and Bros., New York. \$3.50. 8 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; xi + 539 + 2 plates; 1936.

#### LABORATORY MANUAL IN ELEMENTARY HUMAN PHYSIOLOGY.

By Sherburne F. Cook and Mary A. Burmester. Harper and Bros., New York. \$.50. 8 $\frac{1}{2}$  x 5 $\frac{1}{2}$ ; iii + 76; 1935 (paper).

The textbook is up to date and quite comprehensive. What is perhaps even more important, it is so well written that many students will read assignments in it! Unfortunately, there is no bibliography whatsoever and not a reference to help a student follow up a topic that interests him. Also the author, doubtless unwittingly, gives the impression that he has said the last word on every subject covered. Even elementary students will instantly recognize how improbable this is.

The laboratory manual is a paper bound pamphlet giving detailed instructions for a rather well planned series of experiments. Leading questions are asked about each experiment.



#### GRUNDLAGEN DER EPIDEMIOLOGIE.

By Georg Jürgens. Johann Ambrosius Barth, Leipzig. RM. 7.50. 9 $\frac{1}{2}$  x 6 $\frac{1}{2}$ ; ix + 165; 1936 (paper).

This little book divides into four parts. Part I is a discussion of the fundamental principles of infectious diseases, and deals with such subjects as the mechanisms of infection, the incubation period, and

immunity. In Part II the author gives a few partly historical researches on epidemiology. He discusses here the importance of epidemics in public health, and epidemic and endemic infections. Part III is devoted to the origin and spread of an epidemic, the interrelations of epidemics to each other, and the importance of a condition of immunity. In Part IV a section is devoted to the use and misuse of statistics.



**A HANDBOOK OF UROLOGY FOR STUDENTS AND PRACTITIONERS.**

By *Vernon Pennell*. University Press, Cambridge; Macmillan Co., New York.

\$2.75. 7½ x 5; viii + 224; 1936.

This book by a well known English surgeon has been designed to place before the many students and practitioners who have not had post-graduate instructions in this field a short and concise account of urinary diseases, with their method of investigation and treatment. Rare diseases and uncommon and obsolete treatments have been rigorously pruned, and venereal diseases and other infections of the genital tract have been largely omitted. Only those methods now most commonly employed in operating are described. In an appendix is given a list of drugs and preparations for use in urological cases. The volume is illustrated and indexed.



**A LA RECHERCHE DU TEMPS VÉCU. *Actualités Scientifiques et Industrielles*, 288. *Exposés de Physiologie*, VIII.**

By *R. S. Lacaze*. Hermann et Cie, Paris. 12 francs. 10 x 6½; 55; 1935 (paper).

Time as measured by physical instruments does not always correspond to the "time lived" by the living organism. Therefore, in order to understand and study the succession of events that occur in the living organism it is necessary to find a measure of "physiological" time which is independent of "physical" time. And, since the concept of time is a product of the mind, the mechanism which measures it must be sought for in the brain. This is

the essence of the author's thesis which is founded on Bergsonian philosophy. The discussion is in the main theoretical, savours of the metaphysical, and is not easily understandable to the empiricist.



**AUTRES SCENES DE LA VIE ANIMALE. *Voyage en Amérique du Sud. Quatrième édition.***

By *Léon Binet*. Gallimard, Paris. 12 francs. 7½ x 4½; 143; 1935 (paper).

This little book, written by an eminent physiologist, is the elaboration of some notes jotted down on a lecture tour to Argentina and Uruguay. It contains short sketches of some of the aquatic, reptilian, mammalian and avian life of these countries but is concerned rather with physiological implications than natural history. It is interestingly written. Bibliographies are appended to each of the chapters.



**LES PARATHYROÏDES. *Actualités Scientifiques et Industrielles*, 307. *Histophysiologie*, I.**

By *Harald Okkels*. Hermann et Cie, Paris. 10 francs. 10 x 6½; 26; 1935 (paper).

This volume starts a new sub-series of the *Actualités*, under the title *Histophysiologie*, edited by Professor Policard. The author clearly outlines what is known about the parathyroids and their influence on the muscular, nervous and bony systems of the body; their morphology, biochemistry, physiology, and pathology; and discusses preparations containing parathyroid hormones and their standardization.



**LA SECRETION DE L'ADRENALINE SON MÉCANISME NEURO-HUMORAL. *Actualités Scientifiques et Industrielles*, 273. *Exposés de Physiologie*, VI.**

By *B. Ming*. Hermann et Cie, Paris. 12 francs. 10 x 6½; 47; 1935 (paper).

The author has very ably brought together in a small space the results of a large body of material dealing with the secretion of adrenalin. In many cases no attempt is



made towards definite conclusions and controverted opinions are given as such. Although some American workers are included in the four-page bibliography, the greater part is devoted to French, German and English researches.



CHINESE MEDICAL JOURNAL SUPPLEMENT No. 1. *Pathology and Microbiology. Being Mainly Proceedings of the Chinese Society of Pathology and Microbiology held in Canton, November 5-8, 1935.*

*Chinese Medical Journal, Peiping.* \$2.50. 10 x 7; 518 + 75 plates; 1936 (paper).

This first number of the Supplement Series—of the same size and format as the regular issues of the Chinese Medical Journal—has brought together a number of papers on pathology and microbiology. There is also an excellent article on *Methods of Illustrating Scientific Papers*. All of the papers are in English.



ALTERS-FORSCHUNG. *Untersuchungen und Berichte über Lebensdauer, Altern und Tod.* 2 Jahrgang.

*Edited by Josef Kluger. Josef Kluger, Gartenstrasse 135, Wünschelburg-Heuscheuer.* 3 marks. 9½ x 6½; 40; 1936 (paper).

The second volume of this annual devoted to the investigation of senescence and senility contains a brief and rather vague summary of some recent studies on longevity and how to keep from growing old. The last half of the pamphlet, and by far the most useful, is a bibliography of anything concerning longevity that has appeared in the last two years and has come to the editor's attention.



REPORT OF THE PAN-AFRICAN HEALTH CONFERENCE HELD AT JOHANNESBURG, NOVEMBER 20TH TO 30TH, 1935. *League of Nations. Quarterly Bulletin of the Health Organisation. Vol. 5, No. 1.*

*League of Nations. League of Nations, Geneva; World Peace Foundation, New*

*York.* 65 cents. 9½ x 6½; 209; 1936 (paper).



## BIOCHEMISTRY

ALCALOÏDES (*Première Partie*). (*Généralités, Ptomaines et Leucomaines. Drogues a Alcaloïdes Liquides Toxiques. Opium et ses Alcaloïdes*). *Actualités Scientifiques et Industrielles*, 262. *Leçons de Toxicologie VII.*

By René Fabre. Hermann et Cie, Paris. 12 francs. 10 x 6½; 65; 1935 (paper).

ALCALOÏDES (*Deuxième Partie*). (*Des Solanées Mydriatiques, de la Coca, des Aconites, des Strychnées, Liliacées. Généralités*). *Actualités Scientifiques et Industrielles*, 263. *Leçons de Toxicologie VIII.*

By René Fabre. Hermann et Cie, Paris. 12 francs. 10 x 6½; 59; 1935 (paper).

TOXIQUES MINÉRAUX (*Première Partie*). (*Généralités. Arsenic, Antimoine. Actualités Scientifiques et Industrielles*, 292. *Leçons de Toxicologie, IX.*

By René Fabre. Hermann et Cie, Paris. 12 francs. 10 x 6½; 69; 1935 (paper).

TOXIQUES MINÉRAUX (*Deuxième Partie*). (*Mercur, Bismuth, Plomb, Thallium. Actualités Scientifiques et Industrielles*, 293. *Leçons de Toxicologie, X.*

By René Fabre. Hermann et Cie, Paris. 12 francs. 10 x 6½; 57; 1935 (paper).

TOXIQUES MINÉRAUX (*Troisième Partie*). (*Cuivre, Zinc, Chrome, Nickel, Manganèse, Baryum, Radium, Métalloïdes Divers. Actualités Scientifiques et Industrielles*, 294. *Leçons de Toxicologie, XI.*

By René Fabre. Hermann et Cie, Paris. 15 francs. 10 x 6½; 69; 1935 (paper).

This textbook of medicolegal toxicology deals primarily with the relative usefulness of various means of detecting the presence of poisons in human cadavers, principally: alkaloids (to which 120 pages are devoted) arsenic, antimony, mercury, bismuth, lead, thallium, copper, zinc, chromium, nickel, manganese, barium, and radium. For the purposes of the lecture room the treatment is quite satisfactory; the merits and demerits of the commonly employed chemical tests are nicely balanced, and there is a great deal of sound advice intended to keep an ambitious young toxicologist from making a fool of himself in court. It pains us to observe, however,

that a book as interestingly written as this should entirely lack bibliographic citations and an index. Also the author is inclined to be a bit vague about the practical details of laboratory work.



LES SOLUTIONS CONCENTRÉES. *Théorie et Applications aux Mélanges Binaires de Composés Organiques.*

By Jean Timmermans. Masson et Cie, Paris. 130 francs.  $9\frac{1}{2} \times 6\frac{1}{2}$ ; 646; 1936 (paper).

This is an extremely thorough treatise limited to binary solutions of organic compounds in which the two components are present in comparable quantities. It is further restricted by the exclusion of all systems for which there are no data between 10 and 90 gm. per cent, or only one datum between 10-20 gm. per cent or 80-90 gm. per cent, but even so this is a weighty tome. The book is divided into three parts. Part I deals with systems in which there is an analogy of structure between the components; Part II, with components of different chemical types; and Part III with systems in which one of the components includes a hydroxyl group. Each chapter, furthermore, consists of two parts: (1) a clear theoretical discussion with the more abstract points clearly explained by examples; and (2) a series of diagrams (540 in all), many of which include more than one property in the same figure, and lists of solutions, their properties, and discoverers. The author has provided a twenty-six page bibliography and an index of formulae, arranged in the sequence used in Richter's *Lexicon*, beginning with methane,  $\text{CH}_4$  and ending with tristearine,  $\text{C}_{57}\text{H}_{110}\text{O}_6$ . The thoroughness with which this book has been prepared may be noted by an example: reactions for benzene are mentioned in over 300 combinations. Timmermans has rendered a great service to his colleagues in preparing this book.



ANNUAL REVIEW OF BIOCHEMISTRY. *Volume V.*

Edited by James M. Luck. *Annual Review of Biochemistry, Stanford University P.O., Calif.* \$5.00.  $8\frac{1}{2} \times 6$ ; ix + 640; 1936.

The *Annual* is becoming increasingly important to workers in biochemistry. The present volume follows the same general plan of previous volumes and maintains the same high standard. As is customary the authors of the sections differ from time to time, as well as the arrangement of the subject matter. In this issue there has been added a section on X-ray studies on the structure of compounds of biochemical interest. The authors, O. L. Sponsler and W. H. Dore point out that a "complete knowledge of the structure of a given biochemical substance should afford valuable information as to its molecular stereochemistry and should play an important rôle in the solution of such vexing problems as the mechanism of optical rotation and the existence of various ring types among the sugars."

We also note that the vitamins are now treated under two headings. H. von Euler writes on the water-soluble vitamins and E. V. McCollum on the fat-soluble vitamins.

To the student the excellent literature lists accompanying the chapters are invaluable. The volume has an index of author's names but no general index.



MANUEL DE BIOCHIMIE.

By Pierre Thomas. Masson et Cie, Paris. 180 francs.  $10 \times 6\frac{1}{2}$ ; vi + 978; 1936.

This book has been prepared for the use of physicians and biologists who for lack of time have not been able to keep abreast of the advances in biochemistry as published in the large number of technical treatises and journals not devoted to their own field. The author has here brought together a large body of literature and produced an up-to-date manual (to the end of 1935). Directions are included for the latest methods of the preparation and determination of dosages, reactions, and extractions. A table of "practical exercises" and an index are appended.

#### EXPERIMENTAL ENZYME CHEMISTRY.

By Henry Tauber. Burgess Publishing Co., Minneapolis. \$3.50. 10 $\frac{1}{2}$  x 8 $\frac{1}{2}$ , v + 118; 1936.

A mimeographed text, confining itself to the more important of recent researches, and generally eschewing theoretical considerations in order more directly to concentrate upon the experimental aspects of enzyme chemistry. It carries extensive recent bibliographies following each of its eleven chapters. The book is really an admirably condensed review of recent literature, with running directions for laboratory work included in the text. The general biologist will find it useful to have at hand.



TRAITÉ DE CHIMIE ORGANIQUE. Tome II. Fascicule I et II. Propriétés Optiques des Combinaisons Organiques. Structure des Molécules et Spectres d'Absorption. Spectres de Fluorescence. Application des Rayons X à l'Etude des Composés Organiques. Effet Raman. Propriétés Diélectriques et Constitution Chimique. Propriétés Magnétiques et Constitution Chimique. Parachor et Constitution Chimique. Mécanisme des Réactions. Radicaux Libres Organiques. Transpositions Intramoléculaires. Empêchement Stérique. Catalyse. Antioxygènes et Prooxygènes, by P. Ramart-Lucas, A. Andant, M. Auméras, H. Bonnet, M. Bourguet, E. Carrière, E. Darmois, C. Dufraisie, A. Kirmann, J. Lecomte, J. Martinet, C. Mauguin, P. Pascal, L. Piaux, G. Vavon.

Published under the direction of V. Grignard and Paul Baud. Masson et Cie, Paris. 280 francs. 10 x 6 $\frac{1}{2}$ ; xv + 1273; 1936.

This is the third volume to appear of a comprehensive *opus* on organic chemistry ultimately to comprise fifteen volumes. Volumes I and III have already been noticed in these columns in Numbers 1 and 3, respectively, of the current volume. The scope of the two parts noticed here is sufficiently indicated in the subtitle.



ESSAI SUR LA BIOCHIMIE GÉNÉRALE ET COMPARÉE DES PIGMENTS RESPIRATOIRES.

By Jean Roche. Masson et Cie, Paris. 40 francs. 10 x 6 $\frac{1}{2}$ ; 170; no date (paper).

This monograph on the respiratory pigments is approached from the point of view of correlating chemical structure and physiological effect. It is clearly and succinctly written and is addressed not only to specialists but to all those interested in biological problems. An appendix describes methods of preparation for study and methods of measurements. A bibliography of 17 pages is included.



LES PARENTÉS CHIMIQUES DES ÊTRES VIVANTS. *Actualités Scientifiques et Industrielles*, 282. *Exposés de Physiologie*, VII.

By Paule Lelu. Hermann et Cie, Paris. 10 francs. 10 x 6 $\frac{1}{2}$ ; 47; 1935 (paper).

This is a review of the numerous investigations regarding the comparative biochemistry of the different classes of animals. The author discusses briefly but adequately the work of Needham, Arnold and Luck, Clementi and others. He summarizes their results and seeks to demonstrate that certain chemical affinities between different species can be used as a criterion to establish their position in the evolutionary scale.



HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. Lieferung 451. *Fermentforschung*. Containing following articles: *Pektinfermente (Pektinasen)*, by Felix Ehrlich; *Die Isolierung von kristallisiertem Trypsinogen und dessen Umwandlung in kristallisiertes Trypsin*, by M. Kunitz and J. H. Northrop; *Amylase (Nachtrag)*, by Theodor Sabalitschka; *Vereinfachung der Methodik des Nachweises von Abwehrproteinasewirkungen (Nachtrag)*, by Emil Abderhalden.

Urban und Schwarzenberg, Berlin. 13 marks. 10 x 7; 206; 1936 (paper).



#### SEX

MEDICAL HISTORY OF CONTRACEPTION. *Medical Aspects of Human Fertility Series* Issued by The National Committee on Maternal Health, Inc.

By Norman B. Himes. *The Williams & Wilkins Co., Baltimore.* \$7.00. 9½ x 6½, xxxi + 521; 1936.

Dr. Norman Himes has put all students of human biology much in his debt by the production of this substantial treatise. Most students of population problems, including Dr. Himes, adhere to the view that the practice of contraception is virtually the sole causal factor of importance concerned in the widespread decline of human birth rate in the last half century or so. There are still a few hardy souls, of whom the late John Brownlee and Udney Yule in England are notable examples, who have thought the matter less simple than this. But it is obvious that under the circumstances, there is need for a systematic examination of the history of man's ideas and behavior about tampering with the normal functioning of his reproductive mechanisms, to the end that he may enjoy his sexual cake without having to pay for it, as it were. Such a history, carefully wrought, Dr. Himes now provides.

The book starts with ethnological evidence from preliterate societies, goes on to the peoples of antiquity in the western world (Egyptians, Greeks, Romans, and biblical folk), and then to eastern cultures (China, Japan, and India). The next section of the book discusses contraceptive techniques in Europe during the Middle Ages and early modern times. In this section is included a long history of the condom, of which some 317 million are said to be manufactured in the United States annually.

The remainder of the book traces the history of the birth control movement during the 19th century in Europe and America, and an examination of the procedures and statistical results of birth control clinics.

The documentation is extensive, the bibliography covering some 60 pages of 8-point type. Detailed author and subject indexes round out a valuable and useful work.

*Allen and Unwin, London.* 16s. 8½ x 5½; xvi + 367; 1936.

Friendship-love is defined by the author as a mental state of a sublime nature experienced towards a person or group of persons of the same or opposite sex. In contrast, the author believes that a mental state is sexual if it is provoked or directed towards a person of the opposite sex, if reproduction is its purpose, or it is associated with "venereal voluptuousness" or physiologic activity of the sex organs. Having defined (*sic*) his terms, he attempts to prove that in childhood there can exist only friendship-love untainted by the sexual. The evidence to support his thesis is given by the diary of a Russian school boy compiled from the thirteenth to the sixteenth year of age. The diary describes the child's friendship and affection for other boys and girls, his jealousy, and all the other manifestations of the sensitive adolescent mind. Since apparently none of the sensations experienced by the writer of the diary can be classified as sexual, the author concludes that love is entirely independent of the sexual. Aside from the fact that this theory has been the favorite subject of the more idealist philosophers and romantic poets, the evidence presented by the author does not prove his thesis unless it is shown that the writer of the diary set down in it *all* the sensations he experienced. This is doubtful. For example, the author states that the diarist, now an adult, recalls the unique sensation of his first nocturnal emission, yet it is not mentioned in the diary. In fact, from a careful perusal of the diary, it seems the product of a school boy imitating the style of romantic prose writers. Nevertheless it is an interesting document and would be more effective if the author had translated it into literary English instead of attempting a literal translation, even to the point of presenting in English the equivalents of the child's Russian abbreviations.

#### FRIENDSHIP-LOVE IN ADOLESCENCE.

By N. M. Iovetz-Torshchenko. *George*

DÉTERMINISME ET RÉALISATION DANS LE DEVENIR DU SEXE. *Actualités Scientifiques et Industrielles*, 300. *Exposés de Biologie*

(*La Cellule Germinale dans l'Ontogénèse et l'Évolution*), V.

By Vera Dantschakoff. Hermann et Cie, Paris. 18 francs. 10 x 6½; 74; 1935.

In the light of recent experiments on the reversal of sex, this characteristic can no longer be explained as solely due to the genetic constitution of the germ cells or to the balance of sex chromosomes and autosomes. In view of this the author attempts to summarize all the facts on the subject, and from this summary derives the following general proposition on sex determination. The constitution of the germ cell, the decisive agent for the realization of sex, permits a double orientation since it contains both male and female elements. Therefore, the genetic sex characteristics can be realized only when a specific and particular relationship is established between the germ cell and the environmental tissues. In other words, sex is a resultant of genetic and environmental (somatic) factors either of which can be modified.

There is actually nothing new in these statements. However they deserve to be emphasized especially for the benefit of some writers of current textbooks on genetics. The exposition of the author is, as usual, clear and her analysis is well corroborated by facts drawn from her own experimental work and that of others.



FRIGIDITY IN WOMEN. *Its Characteristics and Treatment.*

By Eduard Hitschmann and Edmund Bergler. Translated by Polly L. Weil. Nervous and Mental Disease Publishing Co., Washington. \$2.00. 9 x 6; v + 76; 1936.

In this monograph the authors reiterate the classical Freudian theory regarding the influence of subconscious repressions on sexual behaviour. They classify the causes of frigidity in women into 18 groups, beginning with the Oedipus complex and ending with constitution. Illustrative examples are given and the prognosis for each type of frigidity is discussed. Two typical cases supposedly cured by psycho-analysis are described fully and at length.

## BIOMETRY

GRAPHS. *How to Make and Use Them.*

By Herbert Arkin and Raymond R. Colton. Harper and Bros., New York. \$3.00. 9½ x 6½; xvi + 224 + 1 plate; 1936.

In 1915 a committee of the American Statistical Association attempted to standardize certain procedures related to graphs and graphing. This committee, however, emphasized primarily the theoretical principles involved in making graphs and did not discuss to any extent the technique of construction of the graphs themselves. During the last two decades, although graphs have been used more and more extensively, little attempt has been made to crystallize standards of perfection towards which all authors should strive. The writers of the present volume have attempted to set up these standards and obviously hope that they will be adopted. Whether this will be so seems rather dubious at the moment, since most people have a tendency to continue using the types of graph with which they are familiar regardless of their value or soundness. But in any case this book does give a wealth of practical, understandable material about the usual graphic forms with examples of their adaptability to specific data and suggestions as to their construction. The biologist will find some of the material of little direct use, especially the generous discussions of methods applicable only to business and advertising purposes. Even so, the book is a commendable one and should find supporters among the biometricians as well as other folk interested in picturing quantitative facts.



AN OUTLINE OF BIOMETRIC ANALYSIS.

By Alan E. Trelor. Burgess Publishing Co., Minneapolis. \$3.10. 10½ x 8½; [6] + 193; 1936.

This textbook of statistics has for its purpose to acquaint the student of biometry with the principles underlying some of the more complex forms of analysis. The first part of the book contains a brief introduction to the history of statistics and is followed by a description of the fundamental formulae for the calculation of constants in the case of univariate and

bivariate frequency distributions. Parts 2 and 3 treat of correlational analysis and statistical estimation, including the methods proposed by R. A. Fisher. There is an appendix with some useful tables.

This is without doubt one of the best of the recent textbooks on statistics because the author always states clearly what are the theoretical foundations on which a formula rests. As a result, the student is enabled to realize the limits of applicability of a particular method of analysis. This is sufficient merit to recommend the book as supplementary reading for students of biometry.



#### METHODS OF STATISTICAL ANALYSIS.

By C. H. Goulden. Burgess Publishing Co., Minneapolis. \$3.00. 10 $\frac{3}{4}$  x 8 $\frac{1}{2}$ ; ii + 165; 1936.

The main purpose of this book is to illustrate the applications of R. A. Fisher's methods of analysis. The first two chapters are concerned with elementary statistics: frequency tables, calculation of the mean, the standard deviation, and the constants of a normal curve. The author then proceeds to discuss and give numerous examples of the computations involved in the tests of significance, correlation coefficients, regression, analysis of variance and of covariance, etc.

This book will be found useful by the student already well-grounded in statistics and interested in learning the mechanics of applying the formulae in question. It cannot be recommended for the beginner because the treatment of elementary statistics is too sketchy, the elements of the theory of probabilities have been omitted, and no attempt has been made to elucidate the theoretical foundations and limitations of the formulae discussed.



#### MÉTHODES STATISTIQUES APPLIQUÉES À LA PATHOLOGIE VÉGÉTALE.

By J. Dufrenoy. *Annales des Epiphyties et de Phytogénétique* 1: 147-256 1934-1935 (1936).

There has existed for sometime a need for a comprehensive treatise on the applications

of statistical methods to special fields in plant pathology. Dufrenoy has bridged the gap between the studies of biometricians and the results of the present day investigators in the special field mentioned. Of particular interest are the sections dealing with the reliability of results of the application of fungicides to crop plants under field conditions; with the "causes" which are admittedly complex. Especially good is the emphasis on the way in which the study of distributions permit one to represent the effects of pathological agents. There is a good bibliography and the paper is well indexed.



#### BEITRÄGE ZUR DEUTSCHEN STATISTIK. Festgabe für Franz Zizek zur 60. Wiederkehr seines Geburtstages.

Paul Flakämper and Adolf Blind, Editors. Contributions by Blind, Burkhardt, Flakämper, Gerloff, Grävell, Hecht, Henzel, Jörges, Lind, Lüer, Meyer, Morgenroth, Müller, Schäfer, Seutemann, Vershofen, Winkler and Zahn. Hans Buske, Leipzig. 9 marks. 9 x 6 $\frac{1}{2}$ ; viii + 288; 1936 (paper).

A collection of papers published by students of Professor Zizek in honor of his sixtieth birthday. The contents are arranged under the following heads: General problems of German statistics (four papers); statistical theory (three papers); the organization of statistical boards (two papers); and population and economic statistics (nine papers).



#### PSYCHOLOGY AND BEHAVIOR

PHYSIQUE AND PSYCHOSIS. *An Analysis of the Postulated Relationship between Bodily Constitution and Mental Disease Syndrome. Comparative Psychology Monographs Vol. 13, No. 1, Serial No. 61.*

By Edward M. L. Burchard. Johns Hopkins Press, Baltimore. \$1.25. 10 x 7; 73; 1936 (paper).

This monograph treats of the relationship between somatic characteristics and types of psychoses. In the first part, the author reviews, rather superficially, the extensive

literature which has followed Kretschmer's original publication. He concludes that most of the reports, including Kretschmer's, are subject to criticism from several standpoints and that therefore Kretschmer's hypothesis has yet to be definitely proven or disproven.

The remaining sections of this book contain a description of the author's investigation on 407 male white hospital patients. These include 125 schizophrenics and 125 circulars; the rest constitute a control group. When the patients are classified according to body type it is evident that there exists a positive association between pyknic habitus and circular insanity, and between asthenic habitus and schizophrenia. However, from group comparisons of certain anthropometric measurements and indexes, the author notes that "although significant anthropometric differences appear between the two psychoses, the amount of overlapping is so great that such differences are of very slight or no diagnostic value." As the author well realizes the analysis is incomplete and the results far from novel.



**EFFECTIVENESS OF TOKEN-REWARDS FOR CHIMPANZEES.** *Comparative Psychology Monographs, Vol. 12, No. 5, Serial No. 60.*

By John B. Wolfe. Johns Hopkins Press, Baltimore. \$1.25. 10 x 7; 72; 1936 (paper).

The experiments discussed in this paper were performed with the object of ascertaining whether tokens, in the form of poker chips, could serve as secondary or surrogate rewards for chimpanzees and if so, the relative effectiveness of such tokens in comparison with that of a primary reward, food. The results are based upon the performances of six chimpanzees in various types of tests, although not all of the animals were used in each experiment. Briefly stated, the results of this study "show that tokens came to function as secondary or surrogate rewards for chimpanzees, that in certain situations they were about as effective as food in eliciting certain kinds of behavior, and that chimpanzees can make a variety of discriminations between tokens having different

reward values and can use them in harmony with their drives or motives."



**INFANT BEHAVIOR.** *Comparative Psychology Monographs, Vol. 12, No. 4, Serial No. 59.*

By Mandel Sherman, Irene Sherman and Charles D. Flory. Johns Hopkins Press, Baltimore. \$1.50. 10 x 7; 105; 1936 (paper).

In this study new-born infants ranging in age from several hours to sixteen days were observed for behavior under relatively controlled conditions, utilizing stimuli of varied intensities. Eye responses to light stimuli were observed and also reactions due to sensitivity to pain and to pressure. The strength of hand grasp was measured and several reflexes were tested. It was found that the infant makes many directed movements in response to stimuli of an optimal sort. The results further show that "the adequacy of the pupillary reflex and the reaction to a pain stimulus increases with age, and as a corollary of these observations, the reactivity of an infant, whether reflexive or defensive, is greater the more intense the stimulus."



**COMPARATIVE PSYCHOLOGY.** *A Comprehensive Treatise. Vertebrates.*

By Carl J. Warden, Thomas N. Jenkins and Lucien H. Warner. The Ronald Press Co., New York. \$4.50. 8½ x 5½; x + 560; 1936.

This volume devoted to vertebrates is the last of a three volume comprehensive treatise. It is an excellent review of the more important work which has been done in the field of experimental psychology. It should prove most useful as there is a reference for nearly every statement made and the bibliography is excellent.



**DE OMNIBUS REBUS ET QUIBUSDEM ALIIS**

**OSIRIS.** *Volume I. A Volume of Studies on the History of Mathematics and the History*

of Science. Presented to Professor David Eugene Smith on his 76th Birthday (Jan. 21, 1936).

Edited by George Sarton with the cooperation of R. C. Archibald, B. M. Frick and A. Pogo. Saint Catherine Press, Bruges. 10 x 7; 777; 1936 (paper).

The indefatigable, and truly indispensable, Dr. Sarton starts off *Osiris*, his new companionate journal to the old and honored *Isis*, by devoting the initial volume to a collection of nearly 40 papers about the history of mathematics and related subjects, presented by their authors and the editor as a tribute to Professor David Eugene Smith, who has done so much for the history of science, and its flourishing Society. It is a fine gesture to a worthy recipient.

In format and typography *Osiris* is apparently to be identical with *Isis*. We hope that it may have an equally useful career.

#### A PHILOSOPHY OF SCIENCE.

By Philip Eichler. G. P. Putnam's Sons, New York. \$1.50. 8 x 5½; 111; 1936.

Do you want to know the what, why, and wherefore of motion, gravitation, neuroses, volition, atoms, cancer and all else? Why there are only two sexes, not three? This little book contains the most delightfully confused answers to these questions we have ever had the pleasure of reading. Being naturally curious about such matters, we looked up the explanation of the fair sex: the female, it appears, is "like a line of least resistance."



TEXAS ALMANAC AND STATE INDUSTRIAL GUIDE. Since 1857. Texas Centennial Edition.

The Dallas News, Dallas. 50 cents; 65 cents postpaid. 8½ x 5½; pp. 512 + folding map; 1936 (paper).





# THE PRICES OF BIOLOGICAL BOOKS IN 1936

By RAYMOND PEARL AND MAUD DEWITT PEARL

*Department of Biology, School of Hygiene and Public Health, Johns Hopkins University*

WHEN the QUARTERLY REVIEW OF BIOLOGY began publication in 1926 the custom was inaugurated of reporting at the end of each volume on the cost of the books that had been reviewed in its columns during the year. The present paper, therefore, is the eleventh of these reports on the cost of bio-

logical books. The prices of foreign books have been converted into dollars on the basis of the exchange at the time the books were received. Table 1 shows the findings for 1936, arranged in the customary manner.

reviewed in these columns have aggregated a total of 1,335,258 pages. To American buyers these cost in the aggregate a total of \$14,605.87, leading to an average price per page for the total of 1.094 cents. The weighted average cost per page of 1.147 cents for all the books reviewed in 1936 is 5.4 per cent higher than that for all the books reviewed in our columns during the preceding decade 1926-35 incl., taken as a bulk total. It is higher than the corresponding average for 1935 of 1.032 cents per page by 10.0 per cent. The 1936 average price per page for all books reviewed is 4.6 per cent higher than the corresponding figure for 1926, which was 1.097 cents.

In 1936 the "Other countries" books displaced Germany from her customary position at the head of Table 1, as the source of origin of highest prices for biological books. This is due partly to the fact that the average per page cost of our sample of German biological books fell off a little from the 1935 level, but more particularly because the "Other countries" sample for 1936 included Vosmaer's magnificent monograph on sponges, necessarily very costly to American buyers because of the unfavorable exchange at the time, and inherently so to any buyer because of the expense involved in its superb production. If this item be dropped from the "Other countries" sample, the line in Table 1 would read as follows: Total pages 4491; Total cost \$36.83; Price per page 0.82 cents. Germany would then head Table 1 once more, "Other countries" would drop to seventh place, and all the other countries would

TABLE 1  
*Prices of Biological Books, 1936*

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
Other countries.....	5,366	\$121.33	2.26
Germany.....	7,501	138.01	1.84
British-American.....	7,711	139.20	1.81
British Government....	183	2.97	1.62
France.....	16,503	173.98	1.05
United States.....	89,456	919.27	1.03
Great Britain.....	10,494	97.86	0.94
U. S. Government.....	2,036	4.25	0.21
Totals and weighted average, 1936.....	139,250	\$1,596.87	1.147
Totals and weighted average, 1926-35 incl.....	1,196,008	13,009.00	1.088

logical books. The prices of foreign books have been converted into dollars on the basis of the exchange at the time the books were received. Table 1 shows the findings for 1936, arranged in the customary manner.

The total number of pages reviewed in 1936 is 139,250, a decrease of 2.8 per cent under 1935 but an increase of 68.6 per cent over 1926, the year in which these tabulations began. In the eleven years of the QUARTERLY REVIEW's history the books

otherwise retain their same relative positions.

Table 2 shows the price trends of books published in various countries from 1927 to 1936 and the absolute and relative changes in price from 1935 to 1936 and from 1927 to 1936. In order to keep Table 2 within bounds it is necessary this year to drop off the column for 1926. In the future we shall continue to make this a table showing a decade of prices, but not more. Any reader wishing to refresh his memory regarding the more ancient history of biological book prices

1935 by 14.4 per cent. On the other hand the 1936 average price per page was 5.5 per cent lower than that shown by our 1927 sample. The rise in the per page price of biological books published in France, which has been commented on in these notes in recent years, continued in 1936 and amounted to 22.1 per cent over 1935 prices and 191.7 per cent over those of a decade earlier. Furthermore the 1936 sample of French books was the largest for any single year in the history of the QUARTERLY. Our sample of biological books from British commercial publishers

TABLE 2  
*Comparison of the Prices of Biological Books from 1927 to 1936*

ORIGIN	AVERAGE PRICE PER PAGE										CHANGE + OR - FROM 1935 TO 1936		CHANGE + OR - FROM 1927 TO 1936	
	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	Absolute	Relative	Absolute	Relative
	cents	cents	cents	cents	cents	cents	cents	cents	cents	cents	cents	per cent	cents	per cent
British-American.....	1.39	1.46	1.90	1.91	2.27	1.48	1.29	1.45	1.53	1.81	+0.28	+18.3	+0.42	+30.2
Other countries.....	0.78	1.13*	1.68	0.97	1.53	1.02	0.85	0.86	1.20	2.26	+1.06	+88.3	+1.48	+189.7
Great Britain.....	1.14	1.09	1.29	1.13	1.19	0.89	0.66	0.96	0.84	0.94	+0.10	+11.9	-0.20	-17.5
United States.....	1.09	1.14	1.14	1.09	1.05	1.00	1.02	0.93	0.90	1.03	+0.13	+14.4	-0.06	-5.5
Germany.....	1.20	1.48	1.65	1.82	1.75	1.60	1.43	1.89	2.04	1.84	-0.20	-9.8	+0.64	+53.3
British Government.....	0.96	1.26	0.39	1.19	1.03	1.45	1.39	0.89	0.50	1.62	+1.12	+224.0	+0.66	+68.8
France.....	0.36	0.45	0.47	0.47	0.69	0.60	0.74	1.00	0.86	1.05	+0.19	+22.1	+0.69	+191.7
U. S. Government.....	0.24	0.21	0.23	0.30	0.28	0.36	0.17	0.18	0.11	0.21	+0.10	+90.9	-0.03	-12.5

\* With two special treatises omitted as explained in Vol. 3, p. 601.

can do so by turning up earlier volumes of the Q. R. B.

The average prices per page of our samples of biological books from every origin except Germany were *higher* than in 1935, by amounts ranging from about 12 per cent for books commercially produced in Great Britain to well over 200 per cent for the British Government official publications. This latter percentage means little, however, because the 1936 sample was particularly small, as Table 1 shows. Biological books produced by commercial publishers in the United States in 1936 advanced in average per page price over

TABLE 3  
*Average Biological Book Prices over the Eleven Year Period,  
1926-36 Inclusive*

ORIGIN	TOTAL PAGES	AVERAGE PRICE PER PAGE
British-American.	96,192	1.617
Germany.....	151,569	1.555
Other countries..	46,173	1.364
United States	777,110	1.041
British Government.	7,559	1.031
Great Britain.....	103,934	0.988
France	113,135	0.681
U. S. Government.	39,586	0.144
Total and weighted average.	1,335,258	.094

showed an 11.9 per cent advance in price over the 1935 sample. It is interesting to note, and to emphasize, that Germany alone of all the sources of origin tabled in these reports showed a decline in average per page prices in 1936 as compared with 1935. This is presumably a reflection of the policy put into effect by Germany on Sept. 9, 1935 of granting a 25 per cent reduction in export prices on books and periodicals.

To the present report we add a new feature in Table 3, which sums up by countries of origin the whole eleven years experience of the *QUARTERLY REVIEW*.

A number of interesting inferences may be drawn from this table. In the first place it is evident, from what has now grown to be a substantial sample, that during the past eleven years biological books from all over the world taken together have averaged to cost the American biologist very close to a cent a page, taking good, bad, and indifferent together. Fur-

thermore it is plain that the sources of origin of these books fall into three fairly sharply defined groups relative to unit prices to the American buyer. In the first or relatively high priced group fall books in the British-American, Germany, and "Other countries" categories of origin. The next or medium priced group includes the United States, British Government, and Great Britain (commercial publishers). The average per page cost of biological books has been very nearly the same for these origins. Finally the third or relatively low price group includes books published in France and by the U. S. Government.

The reader should bear in mind that these reports are based on small samples of books in general and, for some countries, on small samples of the biological books published. He should therefore be cautious in applying conclusions drawn from this material to the general domain of book prices.



# INDEX

- Abderhalden, E. (Ed.), Handbook of Biological Methods, 88, 362, 486
- Abnormalities, in cyclopia, 291, 295
- ADELMANN, H. B., The Problem of Cyclopia, 161-182, 284-304
- AGAR, W. E., Whitehead's Philosophy of Organism; an Introduction for Biologists, 16-34
- Albrecht, *et al.*, Pure and Applied Sociology, 466
- Alderman, A. L., Some New and Little Known Amphipods of California, 475
- Aldis, R. W., A Shellac Patent Index, 474
- Alexander, F., and Healy, W., Roots of Crime, 255
- Allen, A. A., American Bird Biographies, 236
- Amblystoma*, 176, 284, 396
- American Committee for Wild Life Protection, The London Convention for the Protection of African Fauna and Flora, 99
- Anderson, E., and Woodson, R. E., The Species of *Tradescantia* Indigenous to the United States, 243
- Androp, S., The Probability of Commitment for a Mental Disorder of any Kind Based on the Individual's Family History, 368
- Arbuthnot, J., More Profit Than Gold, 467
- Arkin, H., and Colton, R. R., Graphs. How to Make and Use Them, 488
- Aron, M., and Grassé, P., Textbook of Zoology, 354
- Auger, D., Rhythms in Action Currents, 461
- Bacteria, nutritional requirements of, 406
- Baitsell, G. A., Manual of Biology, 461
- Baker, J. R., The Chemical Control of Conception, 226
- Balfour-Browne, F., Concerning the Habits of Insects, 238
- Barbour, T., and Porter, M. D., Notes on South African Wild Life Conservation Parks and Reserves, 238
- Barrows, H. R., Elements of General Biology, 460
- Bary, P., *et al.*, Organic Chemistry, 113
- Becker, F. E., 123
- Beebe, W., and Hollister, G., The Fishes of Union Island, Grenadines, British West Indies, with the Description of a New Species of Star-Gazer, 239
- Bengton, N. A., and Van Royen, W., Fundamentals of Economic Geography, 231
- Bennett, W. C., and Zingg, R. M., The Tarahumara, 95
- Benoit, J., The Ovary, 360
- The Testes, 360
- Benson, S. B., A Biological Reconnaissance of Navajo Mountain, Utah, 240
- Beretervide, J. J., and Rosenblatt, S., Endocrine Glands and Prostitution, 115
- Bergmark, D. R., Economic Geography of Asia, 231
- Bergson, H., Thought and the Moving, 120
- Bernatzik, H. A., South Seas, 349
- Bertin, L., Migrations and Metamorphoses of the European Eel, 101
- Besterman, T., A Bibliography of Sir James George Frazer, O.M., 350
- Bews, J. W., Human Ecology, 132
- Bilaterality of eyes, factors responsible for, 289
- Bill, A. C., The Conquest of Death, 112
- Binct, L., Scenes of Animal Life, 483
- Six Lectures on Physiology, 108
- et al.*, Lessons on Medico-Surgical Physiology, 108
- Biochemical and Allied Research in India in 1934, 251
- BIOCHEMISTRY (book reviews), 113, 249, 362, 484
- Biocoenology, 320
- BIOMETRY (book reviews), 115, 252, 365, 488
- Birds, sexual cycle of, 374
- BISMONNETTE, THOMAS H., Sexual Photoperiodicity, 371-386
- Blacklock, D. B., and Southwell, T., A Guide to Human Parasitology, 354
- Black Rock Forest, Black Rock Forest Papers, 477
- Black widow spider, 123
- Boder, D. P., The Influence of Concomitant Activity and Fatigue upon Certain Forms of Reciprocal Hand Movement and Its Fundamental Components, 112
- Bocuf, F., The Scientific Basis of Plant Amelioration, 458
- Bohn, G., The Invertebrates, 100
- Böker, H., Introduction to Comparative Anatomy of Vertebrates, 357
- Bolgert, M., Diseases of the Pancreas and Functional Pancreatic Disturbances, 361
- Bond, W. N., Probability and Random Errors, 365
- Borradaile, L. A., and Potts, F. A., The Invertebrata, 239
- Bose, Sir J. C. (Ed.), Transactions of the Bose Research Institute, Calcutta, 224
- BOTANY (book reviews), 103, 240, 356, 475
- Boulenger, E. G., A Natural History of the Seas, 355
- Bowler, A. C., and Bloodgood, R. S., Institutional Treatment of Delinquent Boys, 464
- Boyd, E., The Growth of the Surface Area in the Human Body, 252
- Braarud, T., The "Ost" Expedition to the Denmark Strait, 106
- Brachet, A., Embryology of the Vertebrates, 358

- Breder, C. M., Jr., The Reproductive Habits of the North American Sunfishes (Family Centrarchidae), 474  
 and Coates, C. W., Sex Recognition in the Guppy *Labietus reticulatus* Peters, 252  
 Bremer, F., *et al.*, Treatise on Normal and Pathological Physiology, 249  
 Brown, G. G., and Hutt, A. McD. B., Anthropology in Action, 95  
 BRUSS, CHARLES T., Aberrant Feeding Behavior Among Insects and Its Bearing on the Development of Specialized Food Habits, 305-319  
 Buffalo Society of Natural Sciences, Bulletin, 223  
 Bull, H. B., The Biochemistry of the Lipids, 250  
 Burchard, E. M. L., Physique and Psychosis, 489  
 BURROWS, WILLIAM, The Nutritional Requirements of Bacteria, 406  
 Buschke, F., X-Ray Studies on Human Twins, 342  
 Bushnell, D. I., Jr., The Manahoac Tribes in Virginia, 231  
 Buthine, M. A., Between the Anvil and the Hammer, 230  
 Buytendijk, F. J. J., The Mind of the Dog, 367  
 Caldwart, D., Essay on the Physical Conception of Life, 225  
 Carbon dioxide, 419  
 Carnegie Institution of Washington, Papers from Tortugas Laboratory of Carnegie Institution of Washington, 470  
 Carrel, A., Man the Unknown, 90  
 Carruthers, D., Arabian Adventure to the Great Nafud in Quest of the Oryx, 469  
 Castetter, B. F., Ethnobiological Studies in the American Southwest, 240  
 Caullery, M., French Science and Its Principal Discoveries Since the Seventeenth Century, 257  
 Modern Conceptions of Heredity, 224  
 Causation, 26  
 Celsus, *De Medicina*, 109  
 Chandler, A. C., Introduction to Human Parasitology, 354  
 CHAPMAN, V. J., The Halophyte Problem in the Light of Recent Investigations, 209-220  
 Chasell, C. F., The Relation Between Morality and Intellect, 462  
 Chen, H. K., Development of the Pectoral Limb of *Necturus maculosus*, 244  
 Cherniss, H., Aristotle's Criticism of Presocratic Philosophy, 256  
 Chideckel, M., The Single, the Engaged and the Married, 365  
*Chinuss Medical Journal*, Chinese Medical Journal Supplement, 484  
 Chisholm, A. H., Bird Wonders of Australia, 234  
 Clephane, I., Towards Sex Freedom, 252  
 Clinton, C. A., Sex Behavior in Marriage, 252  
 Coefficient of dispersion, 322  
 Colloid Committee of the Faraday Society, Collected Scientific Papers of Sir William Bate Hardy, 342  
 Collum, V. C. C., The Tressé Iron-Age Megalithic Monument, 98  
 Compton, A. H., The Freedom of Man, 232  
 Cook, S. F., Elementary Human Physiology, 482  
 and Burmester, M. A., Laboratory Manual in Elementary Human Physiology, 482  
 Copson, E. T., An Introduction to the Theory of Functions of a Complex Variable, 253  
 Corbet, A. S., Biological Processes in Tropical Soils, 85  
 Cornaro, L., How to Live for a Hundred Years and Avoid Disease, 247  
 Cornish, V., Scenery and the Sense of Sight, 246  
 Costanzo, A., Constitution and Mortality, 346  
 Coulter, M. C., The Story of the Plant Kingdom, 242  
 Council on Pharmacy and Chemistry of the American Medical Association, Glandular Physiology and Therapy, 362  
 Cowan, I. McI., A Distributional Study of the *Peromyscus Sitkensis* Group of White-Footed Mice, 240  
 Cranial capacity, 274  
 Creamer, D. B., Is Industry Decentralizing? 97  
 Crile, G., The Phenomena of Life, 344  
 Crozier, W. J., Determinism and Variability in the Behavior of Organisms, 255  
 Cuénot, L., The Species, 222  
 Culver, D. C., Bibliography of Crime and Criminal Justice, 230  
 Cunningham, B. V., Family Behavior, 466  
 Curtius, F., The Organic and Functional Hereditary Diseases of the Nervous System, 248  
 Cutler, D. W., and Crump, L. M., Problems in Soil Microbiology, 85  
 Cyclops, 161, 284  
 experimental production of, 167  
 morphology of, 162  
 Dallas News, Dallas, Texas Almanac and State Industrial Guide, 491  
 Daly, R. A., The Changing World of the Ice Age, 82  
 D'AMOUR, F. B., BECKER, F. E., AND VAN RIPER, W., The Black Widow Spider, 123-160  
 Dampier-Whetham, W. C. D., and Whetham, M. D., Cambridge Readings in the Literature of Science, 257  
 Daniel, R. J., *et al.* (Eds.), Proceedings and Transactions of the Liverpool Biological Society, 86  
 Dantchakoff, V., Sex Determination, 487  
 Daugherty, M., Sex Worship and Disease, 115

- Davis, H. T., and Nelson, W. F. C., Elements of Statistics, 252
- Davis, R. A., Psychology of Learning, 118
- Dawson, L. H. (Eng. Ed.), The March of Man, 227
- Decugis, H., The Destiny of the White Races, 91
- DE OMNIBUS REBUS ET QUIBUSDEM ALIIS (book reviews), 119, 255, 369, 490
- Desbarrolles, A., The Hand and Its Secrets, 349
- Detwiler, S. R., Neuroembryology, 477
- Dhar, N. R. Influence of Light on Some Biochemical Processes, 250
- Dickey, F. van V., Familiar Birds of the Pacific Southwest, 102
- Ditmars, R. L., Serpents of the Northeastern States, 238  
and Bridges, W., Snake-Hunters' Holiday, 235
- Doak, C. C., Evolution of Foliar Types, Dwarf Shoots, and Cone Scales of *Pinus*, 105
- Dodd, S. C., A Controlled Experiment on Rural Hygiene in Syria, 108
- Dodge, C. W., Medical Mycology, 476
- Doeuve, J., *et al.*, Organic Chemistry, 250
- Dog, playing with, 1
- Dollard, J., Criteria for the Life History, 345
- Drew, G. A., A Laboratory Manual of Invertebrate Zoology, 474
- Driesch, H., The Machine and the Organism, 84
- Dublin, L. I., and Lotka, A. J., Length of Life, 229
- Dubuisson, M., The Ionograms of Muscular Contraction, 112
- Dufrenoy, J., Application of Statistical Methods to Plant-Pathology, 489
- Duggan-Cronin, A. M., The Bantu Tribes of South America, 227
- Duggar, B. M., *et al.*, Biological Effects of Radiation, 459
- Dukes, H. H., The Physiology of Domestic Animals, 111
- Eames, A. J., Morphology of Vascular Plants, 476
- Echidna*, 389
- Edgeworth, F. H., The Cranial Muscles of Vertebrates, 357
- Edin, K. A., and Hutchinson, E. P., Studies on Differential Fertility in Sweden, 227
- Efficient causation, 26
- Egypt, Board of Marine Sanitation and Quarantine of, Report on the Pilgrimage to Hedjaz, 148
- Eichler, P., A Philosophy of Science, 491
- von Rickstedt, E. F., Foundations of Race Psychology, 368
- Elliot, C., Rock Garden Plants, 142
- Ellis, H., Psychology of Sex, 364
- Enduring objects, 22
- End-state, 3
- Ephrussi, B., Phenomena of Integration in Tissue Cultures, 87
- Eternal objects, 10
- Extensive continuum, 23
- EVOLUTION (book reviews), 81, 221, 341, 456
- Fabre, René, Medicolegal Toxicology, 484
- Fairgrieve, J., and Young, Ernest, Human Geography, 468
- Feeding behavior of insects, 305
- Fergusson, H., Modern Man, 233
- Ferrets, sexual cycle of, 379
- Fiebiger, J., Animal Parasites, 355
- Fieser, L. F., The Chemistry of Natural Products Related to Phenanthrene, 362
- Final causation, 16
- Fisher, R. A., The Design of Experiments, 116
- Fitzpatrick, F. L., and Horton, R. E., Student's Manual in Biology, 89
- Flaskämper, P., and Blind, Adolph (Eds.), Contributions on German Statistics, 489
- Folsom, J. W., Entomology, 102
- Forest Products Laboratory, U. S. Forest Service, Wood Handbook, 142
- Formosov, A. N., Fluctuations in Numbers of Game Animals, 87
- Franklin Institute, Reports of the Biochemical Research Foundation, 363
- Frenzel, G., Investigations of the Animal World of the Meadow-Lands, 354
- Freud, Sigmund, Autobiography, 134
- Fronmolt, G., Race Problems in Obstetrics and Gynecology, 233
- Frontal sinuses, 169
- Fry, C. C., and Haggard, H. W., The Anatomy of Personality, 468
- Fulton, J. F., A Bibliography of Two Oxford Physiologists, Richard Lower and John Mayow, 361
- Fundulus*, 167
- Furnas, C. C., The Next Hundred Years, 257
- Ganglia, 392
- Gangulee, N., The Indian Peasant and His Environment, 92
- GAUZE, G. F., The Principles of Biocoenology, 320-336  
Experimental Proofs of the Mathematical Theory of the Struggle for Existence, 222
- Gebbing, J., A Life for Animals, 353
- Geipel, G., Introduction to the Genetic Examination of Finger and Hand Prints, 83
- Gene, 57
- GENERAL BIOLOGY (book reviews), 84, 224, 342, 459
- GENETICS (book reviews), 82, 223, 342, 458
- Given, D. H. C., A New Angle on Health, 110

- Glassell, S. A., New or Little Known Crabs from the Pacific Coast of Northern Mexico, 103
- Good, N. E., The Flour Beetles of the Genus *Tribolium*, 470
- Goodrich, C., *et al.*, Migration and Planes of Living, 94
- Gorer, G., Africa Dances, 231
- Goulden, C. H., Methods of Statistical Analysis, 489
- Grabau, A. W., Studies of Gastropoda, 235
- Graham, S. A., The Spruce Budworm on Michigan Pine, 102
- Greaves, J. E., and Greaves, E. O., Elementary Bacteriology, 356
- Greene, E. C., Anatomy of the Rat, 244
- Greenwood, Major, The Medical Dictator and Other Biographical Studies, 465
- Gregory, J., A B C of the Endocrines, 249
- Grignard, V., and Baud, P., Textbook of Organic Chemistry, 486
- Grinnell, J., Differentiation in Pocket Gophers of the *Thomomys bottae* Group in Northern California and Southern Oregon, 240
- Grollman, A., The Adrenals, 480
- Grove, W. B., British Stem- and Leaf-Fungi, 105
- Growth, of man and the great apes, 267  
stimulating substances, 416
- Günther, H., Variability of Organisms and Their Normal Limits, 366
- Guyénot, É., The Determination of Sex and Heredity, 363
- Guyer, M. F., Animal Micrology, 478
- Habitat, black widow spider, 125
- Haglund, S., Life Among the Lapps, 228
- Hale, A. R., The Medical Voodoo, 248
- Hall, E. R., Nevadan Races of the *Microtus montanus* Group of Meadow Mice, 240
- Hall, G. M., Prostitution in the Modern World, 365
- Halliday, W. M., Porclatch and Totem, 230
- Halophyte problem, 209
- Halstead, W., The Effect of Cerebellar Lesions upon the Habituation of Post-Rotational Mystagmus, 246
- Hambly, W. D., Culture Areas of Nigeria, 96
- Hand, proportions of, 434
- Harris, L. J., Vitamins in Theory and Practice, 250
- Hart, A. B., and Cox, I. J., (Am. Eds.), The March of Man, 227
- Hartman, C. G., Time of Ovulation in Women, 365
- Hartman, O., New Species of Spinoidae (Annelida Polychaeta), 475
- Hatt, P., Morphogenetic Processes in the Development of the Vertebrates, 479
- Hayner, J. C., Regional Anatomy, 243
- Head, proportions of, 441
- Health and Efficiency Holiday Annual, 113
- Health Organisation, League of Nations, Quarterly Bulletin, 113, 249
- Hegner, R. W., College Zoology, 472  
Parade of the Animal Kingdom, 99
- Hering, M., The Leaf Burrows of Central and Northern Europe, 239, 474
- Herrick, G. W., Insect Enemies of Shade-Trees, 236
- Hesse, R., Evolution and Darwinism, 457
- Higgins, V., and Marrable, H. T., Cactus Growing for Beginners, 105
- Higher primates and man, 425
- Himes, N. E., Medical History of Contraception, 486
- Hirschfeld, M., Sex in Human Relationships, 251
- Hirschmann, E., and Bergler, E., Frigidity in Women, 488
- Holden, W. C., *et al.*, Studies of the Yaqui Indians of Sonora, Mexico, 348
- Holmes, M. B., An Outline of Probability and Its Uses, 366
- Hort, Sir A. F., Garden Variety, 242
- HOWELL, A. BRAZIER, Morphogenesis of the Shoulder Architecture, Part IV, Reptilia, 183-208
- Howell, A. Brazier, 387
- Hrdlička, A., Melaneans and Australians and the Peopling of America, 232
- Hubbell, T. H., A Monographic Revision of the Genus *Centhophilus*, 470
- Huey, E. G., A Child's Story of the Animal World, 355
- Huey, L. M., A New Silky Pocket Mouse from Sonora, Mexico, 103
- HUMAN BIOLOGY (book reviews), 89, 227, 345, 462
- Huntington, E., *et al.*, Tomorrow's Children, 350
- Hurley, V., Men in Sun Helmets, 350
- Hurst, C. C., Heredity and the Ascent of Man, 81
- Huxley, E., White Man's Country, 94
- Huxley, J. (Ed.), T. H. Huxley's Diary of the Voyage of H. M. S. Rattlesnake, 459
- Huxley, J. S., Problems in Experimental Embryology, 87
- Hyatt, H. M., Folk-Lore from Adams County, Illinois, 98
- Hylobatidae, 270, 433
- Iguana*, morphogenesis of shoulder architecture, 186
- Immunology, 149
- Initial data, 19
- Insects, aberrant feeding behavior of, 305
- Institute of Actuaries and Faculty of Actuaries in Scotland, Continuous Investigation into the Mortality of Assured Lives, 253
- International Federation of Eugenic Organizations, Report of the 11th Assembly, 83
- International Labor Office, Geneva, Occupation and Health, 482

- Iovetv-Tereshchenko, N. M., Friendship-Love in Adolescence, 487
- Iscial callosities in the great apes, 265
- Israeli, N., Outlook upon the Future of British Unemployed, Mental Patients, and Others, 97
- Ivanoff, N. N. (Ed.), Biochemistry of Cultivated Plants, 357
- Ives, J. E., *et al.*, Atmospheric Pollution of American Cities, 461
- Jaffe, B., Outposts of Science, 255
- Jankowsky, W., Blood Relationship, 83
- Järvi, T. H., and Menzies, W. J. M., The Interpretation of the Zones on Scales of Salmon, Sea Trout and Brown Trout, 472
- Jarvis, C. S., *et al.*, Floods in the United States, 461
- Jennings, H. S., Genetics, 81  
Genetic Variations in Relation to Evolution, 223
- Johnson, M. E., and Snook, H. J., Seashore Animals of the Pacific Coast, 473
- Jordan, D. S., A Classification of Fishes, 103
- Jordan, E. O., A Textbook of General Bacteriology, 106
- Jürgens, G., Foundations of Epidemiology, 482
- Kanner, L., Child Psychiatry, 119
- Katznelbogen, S., The Cerebrospinal Fluid and Its Relation to the Blood, 247
- Keep, J., West Coast Shells, 101
- Kelley, T. L., Essential Traits of Mental Life, 367  
and Krey, A. C., Tests and Measurements in the Social Sciences, 96
- Kelway, Phyllis, Hedge Folk in Twilight, 474
- Kemp, P., Healing Ritual, 234
- Kempermann, C. T., Turning Point in Phylogeny, 342
- Kendall, W. C., The Fishes of New England, 236
- Kenly, J. C., Cities of Wax, 239
- Kirk, S. A., Hemispheric Cerebral Dominance and Hemispheric Equipotentiality, 248
- Klauber, L. M., A New Subspecies of *Crotalus confusus*, the Prairie Rattlesnake, 103  
*Crotalus Mitchellii*, the Speckled Rattlesnake, 475
- Klein, W., (Ed.), The Hereditarily Sound and the Hereditarily Diseased, 347
- Klem, Alf, Chemical Analysis of the Samples of Blue Whale Oils, 249
- Kluger, J. (Ed.), Researches on Longevity, 86, 484
- Knapp-Fisher, H. C., The World of Nature, 89
- Kofoid, C. A., *et al.*, The Cycle of Trypanosoma Cruzi in Tissue Culture of Embryonic Heart Muscle, 240
- Koltzoff, N. K., Physiology of Development and Genetics, 84
- Komarov, V. L., The Origin of Plants, 342
- Kostitzin, V. A., Evolution of the Atmosphere, 221
- Krafka, J., A Textbook of Histology, 477
- Krieger, L. C. C., The Mushroom Handbook, 475
- de Kruif, Paul, and de Kruif, Rhea, Why Keep Them Alive? 369
- Kuczynski, R. R., The Measurement of Population Growth, 349
- Külbs, F., Healthy Life, 112
- Lacape, R. S., Physiological Time, 483
- Lakhovsky, G., Cellular Oscillation, 109  
Matter, 119  
The Secret of Life, 109
- Lamond, H. G., An Aviary on the Plains, 354
- Landsteiner, K., The Specificity of Serological Reactions, 358
- Langdon-Brown, Sir Walter, The Integration of the Endocrine System, 359
- Lartschneider, J., Cancer, 113
- Lasorsa, G., The Legitimate Fertility of Women by Age, 115
- Latrodectus*, 127
- Layman, J. D., The Avian Visual System, 361
- League of Nations, Report of the Pan-African Health Conference held at Johannesburg, November 20th to 30th, 1935, 484
- Leakey, L. S. B., Kenya, 464
- Lee, R. E., Man the Universe-Builders, 256
- Lehmann, F. M., Logic and System of the Sciences of Life, 89
- Lelu, P., The Chemical Relationship of Animals, 486
- Lepidoptera, 307
- Lester, P., and Millot, J., The Human Races, 466
- Lévy-Bruhl, L., Primitives and the Supernatural, 93
- Lewin, K., A Dynamic Theory of Personality, 118
- Libby, M. S., The Attitude of Voltaire to Magic and the Sciences, 256
- Liesegang, R. E., Colloid Chemistry for Physicians, 363
- Life, Whitehead's conception of, 31
- Limb, proportions of, 432
- Lincoln, F. C., The Migration of North American Birds, 353
- Lösch, A., Considerations on the Decline in the Birth Rate, 233
- de Loureiro, J. A., Intoxication, 361
- Lovejoy, A. O., and Boss, G., A Documentary History of Primitivism and Related Ideas, 89
- Luck, J. M. (Ed.), Annual Review of Biochemistry, 485
- Lumby, J. R., Salinity and Temperature of the English Channel, 344  
Salinity and Temperature of the English Channel. Atlas of Charts, 344
- Lumière, A., Rebirth of Humoral Medicine, 360
- Lyell, D. D. (Ed.), African Adventures, 351



- Lynn, E., The Red Spears of Honan, 234  
 Lyon, M. W., Jr., Mammals of Indiana, 352
- MacGinitie, G. E., Ecological Aspects of a California Estuary, 226  
 Macmillan, W. M., Warning from the West Indies, 467  
 Madison, H. L., Florida Fishes, 356  
 Turtle Shields, 355  
 Maeterlinck, M., Pigeons and Spiders, 472  
 Maier, N. R. F., and Schneirla, T. C., Principles of Animal Psychology, 254  
 Major, R. H., Disease and Destiny, 359  
 Malinowski, Bronislaw, Coral Gardens and Their Magic, 462  
 Mallet, R., Dementia, 119  
 Maltz, M., New Faces—New Futures, 481  
 Man, characters specific for, 259  
 Mantegazza, P., Physiology of Love, 364  
 The Sexual Relations of Mankind, 114  
 Marett, J. R. de la H., Race, Sex, and Environment, 221  
 Marett, R. R., Head, Heart and Hands in Human Evolution, 81  
 Marie-Victorin, Frère, Some New Statistical Results Concerning the Vascular Plants of Quebec, 476  
 Marshall, C., An Introduction to Human Anatomy, 243  
 MARSHALL, CLYDE, The Functions of the Pyramidal Tracts, 35-36  
 Maximum salinities, 215  
 McComas, H. C., Ghosts I Have Talked With, 253  
 McCrady, E., Reason and Revelation, 456  
 McDougal, W., Religion and the Science of Life, 225  
 McGraw, M. B., Growth: A Study of Johnny and Jimmy, 117  
 McKeown, K. C., Insect Wonders of Australia, 234  
 McKinley, E. B., A Geography of Disease, 245  
 Mellen, I. M., and Lanier, R. J., 1001 Questions Answered about Your Aquarium, 237  
 Mengarelli, C., Constitution in Italian Aristocracies, 96  
 Meyer, A. W., An Analysis of the *De Generatione Animalium* of William Harvey, 471  
 Meyer, B. S., and Anderson, D. B., Laboratory Plant Physiology, 241  
 Mickel, C. E., Mutillidae of the Philippine Islands, 240  
 The Mutillid Wasps of the Islands of the Pacific Ocean, 240  
 Microbiology, Studies from the Laboratories of Microbiology, Nancy, 227  
 Minimum area, 324  
 Minx, B., Secretion of Adrenalin, Its Neuro-Humoral Mechanism, 483
- Mittasch, A., On the Catalytic Factors in Biological Phenomena, 363  
 Molisch, H., Memories and World Impressions of a Natural Scientist, 233  
 de Monfried, H., Hashish, 98  
 Monteil, G., The Egg, 459  
 Morphological conception of gene, 58  
 MORPHOLOGY (book reviews), 107, 243, 357, 477  
 Morton, D. J., The Human Foot, 244  
 Motor-nuclei, 388  
 Muenscher, W. C., Weeds, 103  
 Müller-Freienfels, R., The Evolution of Modern Psychology, 118  
 Muller, H. J., Out of the Night, 348  
 Murphy, R. C., Oceanic Birds of South America, 351  
 Muscles, of shoulder, 194
- Needham, J., Order and Life, 343  
 Neonate activities, 70  
 Nerve-muscle action, 105  
 Nerves, of shoulder, 191  
 Nesbitt, L. M., Desolate Marches, 350  
 Neural plate, 285  
 NEW BIOLOGICAL BOOKS, 81-121, 221-257, 337-370, 456-491  
 Newman, Horatio H., Outlines of General Zoology, 474  
 Newton, W. H. (Ed.), Evans' Recent Advances in Physiology, 481  
 Nexus, 29  
 Norberg, I., Good Food from Sweden, 97  
 Novak, E., The Woman Asks the Doctor, 112  
 Nutritional requirements of bacteria, 406
- Objective datum, 19  
 Odell, C. W., Statistical Method in Education, 117  
 Ogden, B. C., The Herbaceous Flowering Plants, 106  
 Okkels, H., The Parathyroids, 483  
 Optic Anlagen, 175  
 Organism, Whitehead's philosophy of, 16  
 Organization, principles of, 327  
 problem of, 64
- Palazzoli, M., Male Sexual Impotence, 115  
*Paramecium*, 330  
 Parasitic habits, change to phytophagous, 313  
 Pariser, K., Numerical Sex Ratio in Hybrids Obtained by Artificial Fecundation in *Triton*, 458  
 Parker, E., Ethics of Egg-Collecting, 236  
 Patch, E. M., and Howe, H. E., The Work of Scientists, 121  
 Patten, C. A., et al., Sensation: Its Mechanisms and Disturbances, 247  
 Paulian, R., Polymorphism in the Males of the Coleoptera, 101

- Payne, F., and Spieth, E. W., An Open Letter to College Teachers, 256
- Peacock, H. A., Elementary Microtechnique, 107
- PEARL, RAYMOND, and PEARL, MAUD DEWITT, Prices of Biological Books, 492
- Pearse, A. S., The Migrations of Animals from Sea to Land, 353
- Pearson, S. V., The Growth and Distribution of Population, 98
- Pelvis, 425
- Pennell, V., A Handbook of Urology for Students and Practitioners, 483
- Penniman, T. K., A Hundred Years of Anthropology, 345
- Perceptual worlds, 6
- Perry, W. J., The Primordial Ocean, 228
- Peters, C. C., and Van Voorhis, W. R., Statistical Procedures and Their Mathematical Bases, 117
- Peters, J. P., Body Water, 480
- Petersen, W. F., The Patient and the Weather, Vol. 1, Pt. 1, The Footprints of Asclepius, 245 and Milliken, M. E., The Patient and the Weather, Vol. 1, Pt. 2, Autonomic Integration, 479
- Pettingill, O. S., Jr., The American Woodcock *Philobela minor* (Gmelin), 472
- Pettit, A., Antipoliomyelitis Serum Therapy of Animal Origin, 481
- Phillips, M. E., and Cox, L. E., The Teaching of Biology, 86
- Photoperiodicity, 373
- Physiological conception of gene, 60
- PSYCHOLOGY AND PATHOLOGY (book reviews), 108, 245, 358, 479
- Phytophagous habits, change to saprophagous, 312
- Pickard, E. A., Frogs, Toads, and Salamanders, 102
- Pittard, Eugène, Castration of Man and the Morphological Modifications Which Follow, 251
- Playing with a dog, 1
- Pleydell-Bouverie, C., Objective Evolution, 457
- Policard, A., Six Lectures on Normal and Pathological Histophysiology, 478
- Pratt, H. S., A Manual of Land and Fresh Water Vertebrate Animals of the United States, 102
- PRATT, KARL C., Problems in the Classification of Neonate Activities, 70-80
- Predatory habits of insects, 307  
habits, change to phytophagous, 310
- Prehension, 19
- Prenant, M., Textbook of Zoology, 473
- Presiding occasions, 33
- Price, H., A Report on Two Experimental Fire-Walks, 367
- Prices of Biological Books, 492
- Primates, higher, 260
- Principles of biocoenology, 320
- Problem of cyclopia, 161, 284
- Protozoa, experimental biocoenosis of, 331
- Pryor, H. B., Width-Weight Tables, 366
- PSYCHOLOGY AND BEHAVIOR (book reviews), 117, 253, 366, 489
- Puxley, W. L., Deep Seas and Lonely Shores, 461
- Pyramidal tracts, functions of, 35
- Rahn, O., Invisible Radiations of Organisms, 343
- Ranson, S. W., The Anatomy of the Nervous System, 108
- Rayment, T., A Cluster of Bees, 337
- Reproduction, of black widow spiders, 127
- Rice, E. L., An Introduction to Biology, 88
- Rice, T. B., A Textbook of Bacteriology, 104
- Richards, A., and Ortenburger, A. L., Practical Comparative Embryology, 244
- Rippe, I. (Ed.), The Journal of Biological Education, 226
- Rittershaus, Ernst, Constitution or Race? 229
- de Rivas, D., and de Rivas, C. T., Clinical Parasitology and Tropical Medicine, 112
- Roberts, E. A., and Lawrence, J. R., American Ferns, 107
- Roberts, L. J., Nutrition Work With Children, 111
- Roberts, S. H., The Squatting Age in Australia 1835-1847, 463
- Robinson, V. (Ed.), Encyclopaedia-Dictionary of the Sexual Sciences, 364
- Robinson, W. A., Voyage to Galapagos, 348
- Robson, G. C., and Richards, O. W., The Variation of Animals in Nature, 456
- Robson, W. A., Civilization and the Growth of Law, 92
- Roche, J., Monograph on the General and Comparative Biochemistry of the Respiratory Pigments, 486
- Roehl, K. McC., and Newman, H. H., A Laboratory Manual for General Zoology, 474
- Romer, A. S., and Grove, B. H., Environment of the Early Vertebrates, 123
- Rosendahl, C. O., *et al.*, J. Arthur Harris, 475
- van Rossem, A. J., A New Race of Brown Towhee from the Inyo Region of California, 103
- Notes on Birds in Relation to the Faunal Areas of South-Central Arizona, 475
- The Mangrove Warbler of North-Western Mexico, 103
- Ross, R. C., A New Genus and Species of Pigmy Goose from the McKittrick Pleistocene, 103
- Ross, T. A., An Enquiry into Prognosis in the Neuroses, 366
- RUMBLE, E. S., Playing with a Dog, 1-15
- Sabrazès, J., and Saric, R., Mononucleoses, Agranulocytoses, Aleukemic Leukemias, 111

- Salinity, of soil, 109  
 Sarton, George (Ed.), *Osiris*, 490  
 Savory, T. H., *The Arachnida*, 99  
 Scanga, G. (Ed.), *Bulletin of Vocational Guidance*, 468  
 Schebesta, P., and Lebzelter, V., *Anthropology of the Central African Pygmies in the Belgian Congo*, 348  
 Schenk, E. T., and McMasters, J. H., *Procedure in Taxonomy*, 351  
 Schmalhausen, J., *et al.*, (Eds.), *Growth of Animals*, 88  
 Schmidt, H., *Introduction to Palaeontology*, 122  
 Schmidt, P. J., *Anabiosis*, 84  
 Schoenichen, W., *Primeval Germany*, 89, 126, 345  
 School, P., *Sodium Deficiency in Rats*, 114  
 Schrieke, B., *Alien Americans*, 467  
 Schultze, A. H., *Characters Common to Higher Primates and Characters Specific for Man*, 259-283, 425-455  
 Schultz, Br. K., and Hesch, M., *Determination Charts for Eye, Hair and Skin Color*, 350  
 Schulz, B., *Genetics in Medicine*, 458  
 Schulze, K., *Homeopathic Medicines*, 362  
 Scott, G. G., and Kendall, J. I., *The Microscopic Anatomy of Vertebrates*, 107  
 Sears, P. B., *Deserts on the March*, 126  
 Seifriz, W., *Protoplasm*, 345  
 Sensory nuclei, 351  
 Sex (book reviews), 114, 251, 363, 486  
 Sexual photoperiodicity, 371  
 Shapiro, H. L., *The Heritage of the Bounty*, 463  
 Shattuck, G. C. (Ed.), *Handbook of Travel*, 120  
 Sherman, M., *et al.*, *Infant Behavior*, 490  
 Shiras, G., 3d., *Hunting Wild Life with Camera and Flashlight*, 353  
 Shoulder architecture, morphogenesis of, 183  
 Shull, A. F., *Evolution*, 341  
 Shumway, W., *Introduction to Vertebrate Embryology*, 108  
*Silva Fennica*, 357  
 Singer, E., *Fasciae of the Human Body and Their Relations to the Organs They Envelop*, 243  
 Skeleton, of shoulder, 183  
 Slemons, J. M., *John Whitridge Williams*, 232  
 Smilie, W. G., *Public Health Administration in the United States*, 111  
 Smith, K. M., *Plant Viruses*, 106  
 Snodgrass, R. E., *Principles of Insect Morphology*, 107  
 Snyder, T. E., *Our Enemy the Termite*, 352  
 Societies, 30  
 Spaulding, E. G., *A World of Chance*, 369  
 Speck, F. G., *Naakapi*, 94  
 Speransky, A. D., *A Basis for the Theory of Medicine*, 359  
 Spider, black widow, 123  
 Spinal accessory nerve and its musculature, 387  
     column, of primates, 278  
 Stabilization, 329  
 Stafford, G. T., *et al.*, *Individual Exercises*, 113  
 STRAUS, WILLIAM L., and HOWELL, A. BRAZIER, *The Spinal Accessory Nerve and Its Musculature*, 387-405  
 STRÖBER, W. F. H., *The Gene, Its Function and Its Meaning in Genetics*, 57-69  
 Subjective aim, 19  
     form, 25  
 Sumner, W. G., *Essays of*, 93  
 Sutherland, H., *Laws of Life*, 349  
 Sutton, G. M., *The Juvenal Plumage and Postjuvenal Molt in Several Species of Michigan Sparrows*, 102  
 Swiss Society of Anthropology and Ethnology, 350  
 Széchenyi, Count Z., *Land of Elephants*, 351  
 Tauber, H., *Experimental Enzyme Chemistry*, 486  
 Taussig, F. J., *Abortion*, 346  
 Taylor, C. C., *Agriculture in Southern Africa*, 97  
 Taylor, W. P., *Ecology and Life History of the Porcupine (*Erethizon Epixanthum*)*, 238  
 Tchernavin, T., *We Soviet Women*, 129  
 Tee-Van, J., *et al.*, *Scientific Contributions of the New York Zoological Society*, 240  
 Thomas, M., *Plant Physiology*, 241  
 Thomas, P., *Manual of Biochemistry*, 485  
 Thoms, H., *Classical Contributions to Obstetrics and Gynecology*, 249  
     *The Obstetric Pelvis*, 244  
 Thomson, D. F., *Birds of Cape York Peninsula*, 473  
 Thorndike, E. L., *et al.*, *Adult Interests*, 117  
 Tian, A., and Roche, J., *Textbook of Chemistry*, 363  
 Tilden, J. E., *The Algae and Their Life Relations*, 104  
 Timirjaseff-Institute for Biology, Moscow, *Problems of Theoretical Biology*, 344  
 Timmermans, J., *Binary Solutions of Organic Compounds*, 485  
 Todd, J. C., and Sanford, A. H., *Clinical Diagnosis by Laboratory Methods*, 113  
 Toxicity, 137  
 Toxicology, 153  
 Treadwell, A. L., *Polychaetous Annelids from the Vicinity of Nonsuch Island, Bermuda*, 474  
 Treloar, A. E., *An Outline of Biometric Analysis*, 488  
*Triton*, 179, 289  
 Tsang, Yü-Chüan, *The Functions of the Visual Areas of the Cerebral Cortex of the Rat in the Learning and Retention of the Maze*, 255  
 Tveraaen, I., *Contributions to the Study of Whale Oils*, 249  
 Ungerer, E., *Periodic Phenomena in Biology*, 460

- University of Colorado Studies, 121
- Uvarov, B. P. (Ed.), *The Locust Outbreak in Africa and Western Asia in 1934*, 235
- van Uven, M. J., *Mathematical Treatment of the Results of Agricultural and Other Experiments*, 253
- Valence, 3, 9
- Van Riper, W., 123
- Vavilov, N. I. (Ed.), *Theoretical Basis of Plant Breeding*, 82
- Verdoorn, Fr. (Ed.), *Chronica Botanica*, 104
- Verhulpen, E., *Baluba and the Balubais of Katanga*, 465
- Vertebrae, coccygeal, 273
- Viischer, M. B., and Smith, P. W., *Experimental Physiology*, 120
- Volterra, V., and d'Ancona, U., *Biological Associations from the Mathematical Point of View*, 88
- Vosmaer, G. C. J., *The Sponges of the Bay of Naples, Porifera Incalcaria*, 469
- Waddington, C. H., *How Animals Develop*, 478
- Wade, J. S., *A Contribution to a Bibliography of the Described Immature Stages of North American Coleoptera*, 237
- Waksman, S. A., *Humus*, 356
- Walton, E. P., and Foss, P. E., *Social Biology*, 460
- Wardel, R. A., *General Entomology*, 471
- Warden, C. J., *The Emergence of Human Culture*, 457  
*et al.*, *Comparative Psychology*, 254, 490
- Watkins, A. E., *Heredity and Evolution*, 342
- Weber, E., *Introduction to the Statistics of Variation and Genetics*, 253
- Wechsler, D., *The Range of Human Capacities*, 115
- Wegner, R. N., *Indian Races and Vanished Cultures*, 96
- Weisenburg, T., *et al.*, *Adult Intelligence*, 368
- Weling, A. N., *The Karkaris*, 98
- Wellhouse, W. H., and Hendrickson, G. O., *College Biology*, 461
- Westaway, F. W., *The Endless Quest*, 120
- Whedon, W. F., *Spawning Habits of the Mussel *Mytilus Californianus* Conrad*, 475  
 and Kofoid, C. A., *Dinoflagellata of the San Francisco Region*, 475
- Wheeler, W. M., *A Notable Contribution to Entomology*, 337-341
- Whetham, M. D., 257
- White, C. L., and Renner, G. T., *Geography. An Introduction to Human Ecology*, 465
- White, F. W., *Birth Control and Its Opponents*, 114
- Whitehead's philosophy of organism, 16
- Whitfield, F. G. S., and Wood, A. H., *An Introduction to Comparative Zoology*, 100
- Whitnall, S. E., *The Study of Anatomy*, 479
- Whitney, L., *Primitivism and the Idea of Progress*, 233
- Williams, J. F., *Atlas of Human Anatomy*, 478
- Williams, J. J., *S. J., Africa's God, I—Gold Coast and Hinterland*, 468
- Willmer, E. N., *Tissue Culture*, 87
- Willoughby, C. C., *Antiquities of the New England Indians*, 228
- Wishart, J., and Sanders, H. G., *Principles and Practice of Field Experimentation*, 241
- Wodehouse, R. P., *Pollen Grains*, 240
- Wolf, A., *A History of Science, Technology, and Philosophy in the 16th and 17th Centuries*, 119
- Wolf, B., *Catalogue of Cavern Fauna*, 103
- Wolfe, J. B., *Effectiveness of Token-Rewards for Chimpanzees*, 490
- Woodruff, L. L., *Foundations of Biology*, 460
- Wright, F. S., *Report on the Maldon (Essex) Periwinkle Fishery*, 355  
*Conditions of Certain of the Oyster Beds in the South Wales Sea Fisheries District*, 355
- Wright, G. M., and Thompson, B. H., *Fauna of the National Parks of the United States*, 100
- Wrist bones, 271
- Wurmser, R., *Electroactivity in Cellular Chemistry*, 114
- Zilboorg, G., *The Medical Man and the Witch during the Renaissance*, 91
- Zirkle, C., *The Beginnings of Plant Hybridization*, 223
- Zoethout, W. D., *A Textbook of Physiology*, 247
- Zondek, H., *The Diseases of the Endocrine Glands*, 110
- ZOOLOGY (book reviews), 99, 234, 351, 469



